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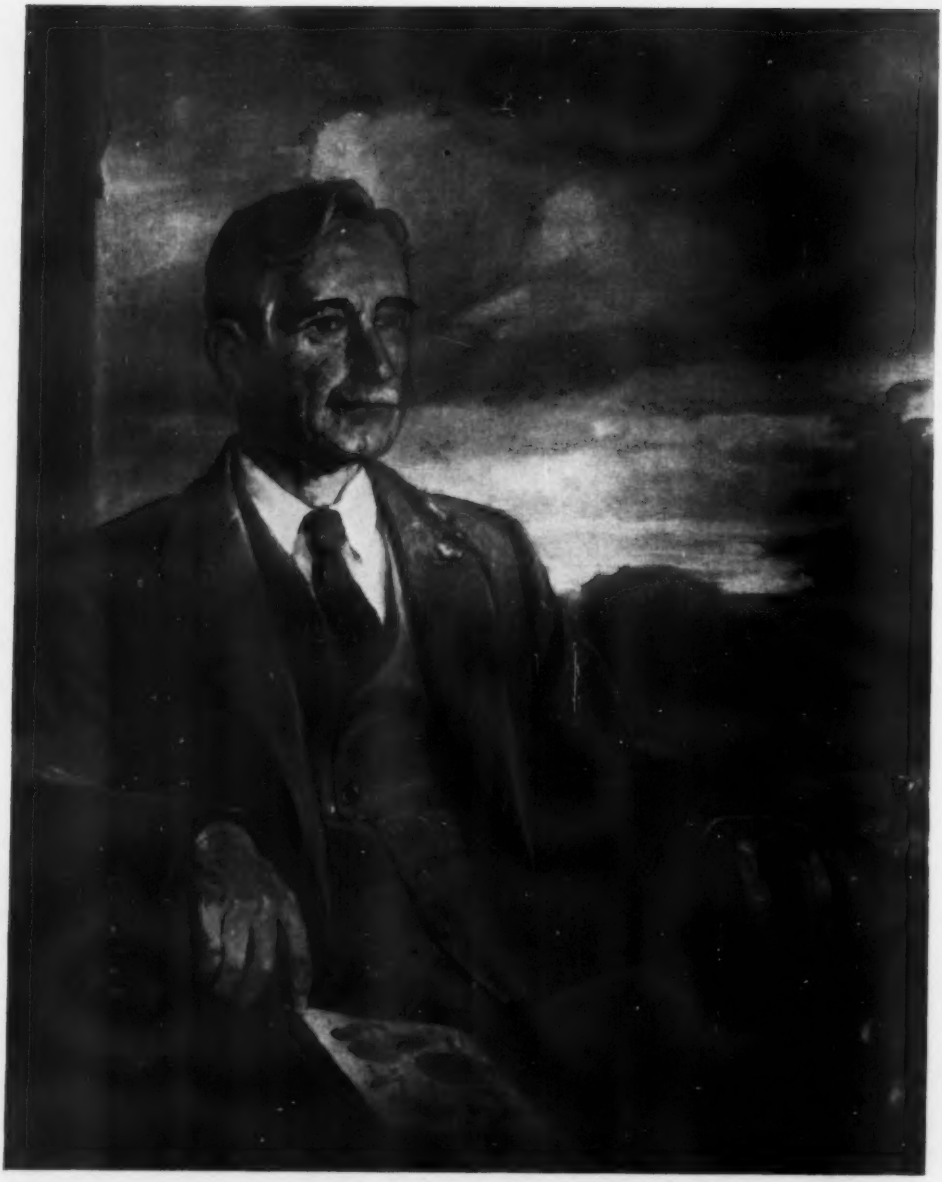

WILLIAM CHAMBERS COKER

From a portrait painted by Arthur W. Bye

TO

WILLIAM CHAMBERS COKER, PH.D., LL.D.

KENAN PROFESSOR EMERITUS OF BOTANY

IN

THE UNIVERSITY OF NORTH CAROLINA

WHO FOR FORTY-ONE YEARS (1904–1945) WAS EDITOR-IN-CHIEF

OF

THE JOURNAL OF THE

ELISHA MITCHELL SCIENTIFIC SOCIETY

This Volume is Affectionately Dedicated

JOURNAL
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Volume 62 June, 1946 No. 1

SOME MARINE ALGAE NEW TO BEAUFORT, NORTH CAROLINA

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Durham, North Carolina

Plates 1–3 and One Text Figure

Since the publication of Hoyt's report in 1920 on the marine algae of Beaufort, N. C., and adjacent regions, no general systematic study on the marine algae of the middle Atlantic Coast of the United States has been undertaken. Wolfe carried on an investigation on diatoms at Beaufort for a few years prior to his death in 1920, the results of which were prepared for publication by Cunningham (1930). In 1943, Blomquist and Pyron published a paper on marine algae washed ashore on Bogue Beach as a result of a hurricane which devastated Charleston, S. C., in the summer of 1940. A few of the species included in this paper had been reported from this vicinity the previous year by Humm (1942).

With the establishment of the Duke Marine Laboratory at Beaufort in 1938, collecting of marine algae was resumed in this area. However, most of this collecting has been incidental to teaching summer classes in algae or in connection with investigations on sources of agar and on agar-digesting bacteria (Humm *et al*, 1946). Despite this unsystematic collecting, a surprisingly large number of algae new to this area has been encountered.

One habitat rich in noteworthy new forms is the outer shore line of Harker's Island. This consists in part of an exposure of a peaty deposit of recent geologic time, known locally as "black rock," which on its outer margin has been eroded by wave action into irregular depressions of varying dimensions (Fig. 1). Its composition is a mixture of sand and enough organic material to give it a dark brown to blackish color. This material forms a unique habitat for algae, which, on the basis of atmospheric exposure, salinity and wave action may be divided into two fairly distinct zones. The upper is above mid-tide level and is, therefore, exposed and free from wave action most of the time. Also during low tides it may be slightly brackish because of seepage of freshwater from the sandbank above. This zone is inhabited mostly by Myxophyceae, such as *Entophysalis granulosa* Kütz., *Microcoleus chthonoplastes* (Mert.) Thur., *Spirulina subsalsa* Oerst., *Lyngbya semiplena* (C. Ag.) J. Ag. and others. The lower zone, which extends from mid-tide to below low-tide level, is constantly subjected to wave action. It is inhabited by such summer forms as, *Pylaiella fulvescens* (Schousb.)

Born., *Sphacelaria furcigera* Kütz. and *S. tribuloides* Mengh., *Ectocarpus duchassaingianus* Grün., *Enteromorpha flexuosa* (Wulf.) J. Ag. and *E. plumosa* Kütz., *Cladophora* spp.; and such winter forms as, *Ectocarpus siliqulosus* (Dillw.) Lyngb., *E. confervoides* (Roth) LeJol. and *Polysiphonia nigrescens* (Huds.) Grev.

The other habitat which has contributed several genera and species new to the region is sea buoys. Most of these forms are of tropical and subtropical affinities. An opportunity for collecting on these buoys has been provided through the United States Coast Guard Aid-to-navigation Service. Collections were made from several buoys between Cape Lookout Shoals and New River when they were hoisted aboard ship to be cleaned and repainted. Most of these buoys are from

Fig. 1. Exposed and eroded peat bed at the east end of Harker's Island near Beaufort, N. C., photographed at low tide.

5 to 20 miles off shore and in from 40 to 100 feet of water. Secchi disk readings at most of the locations of the buoys ranged from 15 to 60 feet. Thus the environmental factors for some of these algae include unusual clarity of water, open sea salinity of only slight variability, and a fairly even water temperature the year around because of the proximity of the Gulf Stream.

New forms encountered on buoys are *Oscillatoria subuliformis* Gom., *Calothrix scopulorum* C. Ag. *ex* Born. and Flah., *Bryopsis pennata* Lamour., *Sphacelaria furcigera Kütz.*, *Colpomenia sinuosa* (Roth) Derb. and Sol., *Gracilaria mamillaris* (Mont.) Howe, *Spyridia aculeata* (Schimp.) Kütz. var. *disticha* Børg., and *Antithamnion cruciatum* (C. Ag.) Nägeli var. *radicans* (J. Ag.) Collins and Hervey.

A total of 28 entities new to the Beaufort area has been determined. Since these represent 2 orders, 4 families and 11 genera new to Beaufort, it seemed

worth while to prepare a report at this time. As collecting and study continue, others will no doubt be added from time to time.

For the benefit of those who may not have access to literature, most of the forms listed below have been illustrated. All drawings were made from material on which the determinations were based.

MYXOPHYCEAE[1]

Order Chroococcales.

Family Entophysalidaceae.

Entophysalis granulosa Kütz. On sand grains on surface of exposed peat above high water, outer beach, Harker's Island, Blomquist, Aug. 25, 1945.

Distribution: Connecticut, North Carolina, Bermuda, Bahamas, Puerto Rico; Europe.

Order Chamaesiphonales.

Family Pleurocapsaceae.

Hyella caespitosa Born. and Flah. Figs. 2, 3. On oyster shells with *Calothrix crustacea*, Piver's Island, Blomquist, June 26, 1945.

Distribution: North Carolina, Florida, Bermuda, Bahamas, Puerto Rico; California (?).

Order Hormogonales.

Family Oscillatoriaceae.

Oscillatoria subuliformis Gom. Fig. 4. On buoy, New River Lighted Whistle Buoy, Humm, Aug. 21, 1944. The specimen had a bright red color. According to Drouet, this species is rare in North America.

Distribution: Massachusetts, North Carolina; Europe.

Spirulina subsalsa Oerst. In moist, brackish beach sand, Mullet Pond, Shackleford Banks, Blomquist, March 13, 1938; on surface of exposed peat, outer beach, Harker's Island, Blomquist, Aug. 25, 1945.

Distribution: Connecticut, North Carolina, Florida, Bermuda. Cosmopolitan.

Lyngbya majuscula Harvey *ex* Gom. Fig. 5. Large mass adrift at Cape Lookout, Humm, Sept. 20, 1941.

Distribution: New England to Florida, Bermuda, West Indies. Widely distributed in subtropical and tropical waters.

Family Rivulariaceae

Calothrix crustacea Born. and Flah. Fig. 6. On oyster shells, Piver's Island, Blomquist, June 26, 1945; on snail shell, Harker's Island, Blomquist, June 28, 1945.

Distribution: New England, North Carolina, Florida, Bermuda, West Indies; California. Cosmopolitan.

Calothrix confervicola C. Ag. *ex* Born. and Flah. Fig. 7. Epiphytic on *Sargassum filipendula* C. Ag., Piver's Island, Blomquist, June 27, 1945.

[1] The Myxophyceae have been determined by Drouet.

Distribution: New England, North Carolina, Florida, Bermuda, West Indies. Cosmopolitan.

Calothrix scopulorum C. Ag., *ex* Born. and Flah. Fig. 8. On buoy mixed with other algae, Cape Lookout Shoal Station Buoy No. 14, Humm, Aug. 21, 1944.

Distribution: New England, North Carolina, Florida, Bermuda, Bahamas, West Indies; California. Cosmopolitan.

Dichothrix fucicola (Kütz.) Born. and Flah. Fig. 9. In their paper on drifting seaweeds, Blomquist and Pyron reported *D. penicillata* Zanard. *ex* Born. and Flah., growing epiphytically on *Sargassum natans* (L.) Meyen. Recently Drouet has examined this material and reports that this represents *D. fucicola*.

Distribution: North Carolina, Florida, Bermuda, Bahamas, West Indies.

CHLOROPHYCEAE

Order Ulotrichales.

Family Ulotrichaceae.

Ulothrix flacca (Dillw.) Thur. Fig. 10. Growing attached to piece of dead *Gracilaria* sp. in shallow water, Bald Hill Bay, Shackleford Banks, Humm, April, 1944. The specimen was sporulating.

Distribution: This alga has a northern range and has not previously been reported south of New Jersey. St. Lawrence to New Jersey, North Carolina; Europe.

Order Ulvales.

Family Ulvaceae.

Enteromorpha lingulata J. Ag. This alga was assigned to *E. prolifera* (Müll.) J. Ag. by Hoyt. Taylor, however, reports (in lit.) that this represents *E. lingulata*. It occurs in two forms apparently related to seasons. The summer form is small, not over a few cm., while the autumn and winter form attains a length of 30 cm. or more. Several collections.

Distribution: Since this species has been confused with *E. prolifera*, its distribution, especially in the northern West Atlantic, is not well known. North Carolina, Texas, Yucatan, Haiti, Puerto Rico, British West Indies, and Venezuela.

Enteromorpha plumosa Kütz. This species was first found attached to a floating golf ball stranded on Bogue Beach, Aug. 8, 1944. Later it was found growing mixed with *Pylaiella fulvescens* and *Sphacelaria* spp. on exposed peat at Harker's Island, Sept. 2, 1944.

Distribution: Nova Scotia; New England to Florida and Texas; Bermuda through the Bahamas and the West Indies to the Virgin Islands.

Order Siphonales.

Family Bryopsidaceae.

Bryopsis pennata Lamour. On buoy, Cape Lookout Shoal Lighted Buoy No. 4, Humm, Aug. 9, 1943.

Distribution: This is so far as known the northern range limit of this species. North Carolina, Florida, Bermuda, Bahamas, West Indies, Barbados, Netherlands West Indies, Colombia.

Bryopsis hypnoides Lamour. Entangled among other algae, Beaufort Harbor, Blomquist, June 26, 1943. Specimens assigned to this species are occasionally encountered during the summer months. They are characterized by having the ultimate branches more or less irregularly placed and not strictly distichous as in *B. pennata* and *B. plumosa* (Hudson) C. Ag. The latter reaches its highest development in the winter months, while the other two are summer forms.

Distribution: New England to Florida, Bermuda, Bahamas, West Indies and Virgin Islands.

PHAEOPHYCEAE

Order Ectocarpales.

Family Ectocarpaceae.

Pylaiella fulvescens (Schousb.) Born. Fig. 11. This interesting species was first collected at Beaufort, N. C., by Karling (1942) while engaged in a study of parasitic organisms on marine algae. This record was reported by Karling in a footnote (1944, pp. 38–39). It was the second reported occurrence of this alga on continental North America. Since Karling's paper deals with very different organisms, it seems best to report it here also. This alga seems to be a permanent summer resident, growing on the outer edge of exposed peat on Harker's Island, associated with *Sphacelaria* spp., *Enteromorpha plumosa*, *Cladophora* spp. etc., and occasionally in Beaufort Harbor. It has not been observed to produce spores at Beaufort.

Distribution: Maine, North Carolina, Bermuda, Bahamas, Puerto Rico, Virgin Islands, Brazil; Morocco, southern France and Spain.

Ectocarpus coniferus Børg. Fig. 12, 13. Epiphytic on *Sargassum filipendula*, Piver's Island, Blomquist, June 27, 1945.

Distribution: This species was originally described from the Virgin Islands. Since then it was found in Bermuda by Collins and Hervey (1912) who said, "... its occurrence in Bermuda is of interest, indicating that it may be found at other stations in the Atlantic." North Carolina becomes the first station for its occurrence on the continental coast.

Order Sphacelariales.

Family Sphacelariaceae.

Sphacelaria furcigera Kütz. Fig. 14. On exposed peat, mixed with *S. tribuloides*, *Pylaiella fulvescens* etc., Harker's Island, Blomquist, Aug. 4, 1944; on buoy, Cape Lookout Shoal Obstruction Lighted Bell Buoy W, Humm, Sept. 19, 1944. This alga was to be expected at Beaufort, since this locality is included in its range.

Distribution : Massachusetts, North Carolina, Bermuda, Florida.

Sphacelaria tribuloides Mengh. Fig. 15. Same habitat as the above, Harker's Island, Blomquist, Aug. 4, 1944.

Distribution: So far as known, North Carolina is the northern range limit of this alga on the Atlantic Coast of North America. Florida, Bermuda, Bahamas, West Indies, Virgin Islands, Barbados, Mexico; Europe.

Order Punctariales.

Family Encoeliaceae.

Colpomenia sinuosa (Roth) Derb. and Sol. Fig. 16, 17. On buoy, Cape Lookout Shoal Obstruction Lighted Bell Buoy W., Humm, Sept. 19, 1944

Distribution: North Carolina becomes now the northern limit of its range in the West Atlantic. Florida; Bermuda through Bahamas and West Indies to Virgin Islands and Panama; Brazil, Argentina; Alaska to Southern California.

Scytosiphon lomentaria (Lyng.) J. Agard. var. *complanatus* Rosenvinge Fig. 18–20. This alga was collected for the first time in North Carolina at Fort Fisher by Louis G. Williams, March 15, 1941. It was collected in Beaufort Harbor on Town Marsh Flat by Humm, Dec. 13, 1944, and again by Humm and Causey, April 23, 1944. Evidently it appears here only in winter and spring as the species does in Bermuda (Collins and Hervey, 1917). All material of this alga from North Carolina is small, does not have marked constrictions typical of the species, and is occasionally twisted. In these characters it agrees with this variety as described by Taylor (1937) and by Smith (1944).

Distribution (of the variety): Greenland, Connecticut, Long Island, North Carolina; California. The species ranges from Lower St. Lawrence to South Carolina and to Bermuda; also in California; Chile.

RHODOPHYCEAE

Order Gigartinales.

Family Gracilariaceae.

Gracilaria mamillaris (Mont.) Howe. Fig. 21, 22. On buoy, Cape Lookout Shoal Obstruction Lighted Bell Buoy L., Humm, Sept. 19, 1944. This tropical species has not previously been observed north of Dry Tortugas (Taylor, 1928) where it was dredged "in moderately deep water." Its occurrence at Beaufort, therefore, represents a remarkable northern range extension.

Distribution: North Carolina, Florida, Yucatan, Bermuda, Puerto Rico, Guadeloupe, Panama, Netherlands West Indies, Venezuela.

Family Gigartinaceae

Gigartina acicularis (Wulf.) Lamour. Fig. 23, 24. Shackleford Banks, Blomquist, Nov. 11, 1940; Humm, Sept. 3, 1944. This alga appears to be a fairly common permanent resident on rock jetties where it grows in mats among other algae. It evidently reaches its peak of development in late summer.

Distribution: North Carolina, Florida, Bermuda, Virgin Islands, Brazil; Europe, Indian Ocean, Australia.

Order Ceramiales.

Family Ceramiaceae.

Antithamnion cruciatum (C. Ag.) Nägeli var. *radicans* (J. Ag.) Collins and Hervey. Fig. 25. On buoy mixed with other algae, Cape Lookout Shoal Station Buoy No. 14, Humm, Aug. 21, 1944.

Griffithsia tenuis C. Ag. Fig. 31, 32. Bald Hill Bay, Shackleford Banks, Humm and Causey, April 18, 1944. This species was reported by Blomquist and Pyron (1943). The present report is, however, based upon attached plants. It has a wide distribution so it is not surprising that it should be found at Beaufort, N. C.

Distribution: Southern Massachusetts to New Jersey, North Carolina, Florida, Bermuda, Bahamas, Virgin Islands; Adriatic, Ceylon, Australia.

Spyridia aculeata (Schimp.) Kütz. var. *hypnoides* J. Ag. Fig. 26–29. Several collections. This is the most common form of this genus at Beaufort and reaches its highest development in early spring and again in autumn. Fragments of it are, however, found fairly frequently throughout the summer. Duplicates of the material reported as *S. filamentosa* by Hoyt have been examined and found to be this species.

Distribution: North Carolina, Florida, Bermuda, Bahamas, West Indies, Virgin Islands, Netherlands West Indies, Venezuela.

Spyridia aculeata (Schimp.) Kütz. var. *disticha* Børg. A form of this species collected on Cape Lookout Shoal Station Lighted Buoy No. 4 by Humm, Aug. 9, 1943, agrees fairly well with this variety.

Distribution: North Carolina, Virgin Islands.

Spyridia filamentosa (Wulf.) Harv. Fig. 30. On pier, Piver's Island, Humm, Sept. 22, 1943; Bald Hill Bay, Shackleford Banks, Humm and Causey, April 20, 1944.

Distribution: This widely distributed species is very common in tropical and subtropical waters. Massachusetts to Florida, Bermuda through Bahamas, West Indies to South America.

Family Rhodomelaceae.

Bostrychi rivularis Harv. Fig. 33, 34. Attached to base of *Dictyota dichotoma* (Huds.) Lamour. on jetties, Shackleford Banks, Humm, Aug. 11, 1945. This alga was included in Hoyt's report although he had not actually observed it at Beaufort. His reason for including it was that he found it "very abundant in harbor, Southport, N. C." and, therefore, was to be expected at Beaufort.

Distribution: New England to Florida, Bermuda, West Indies.

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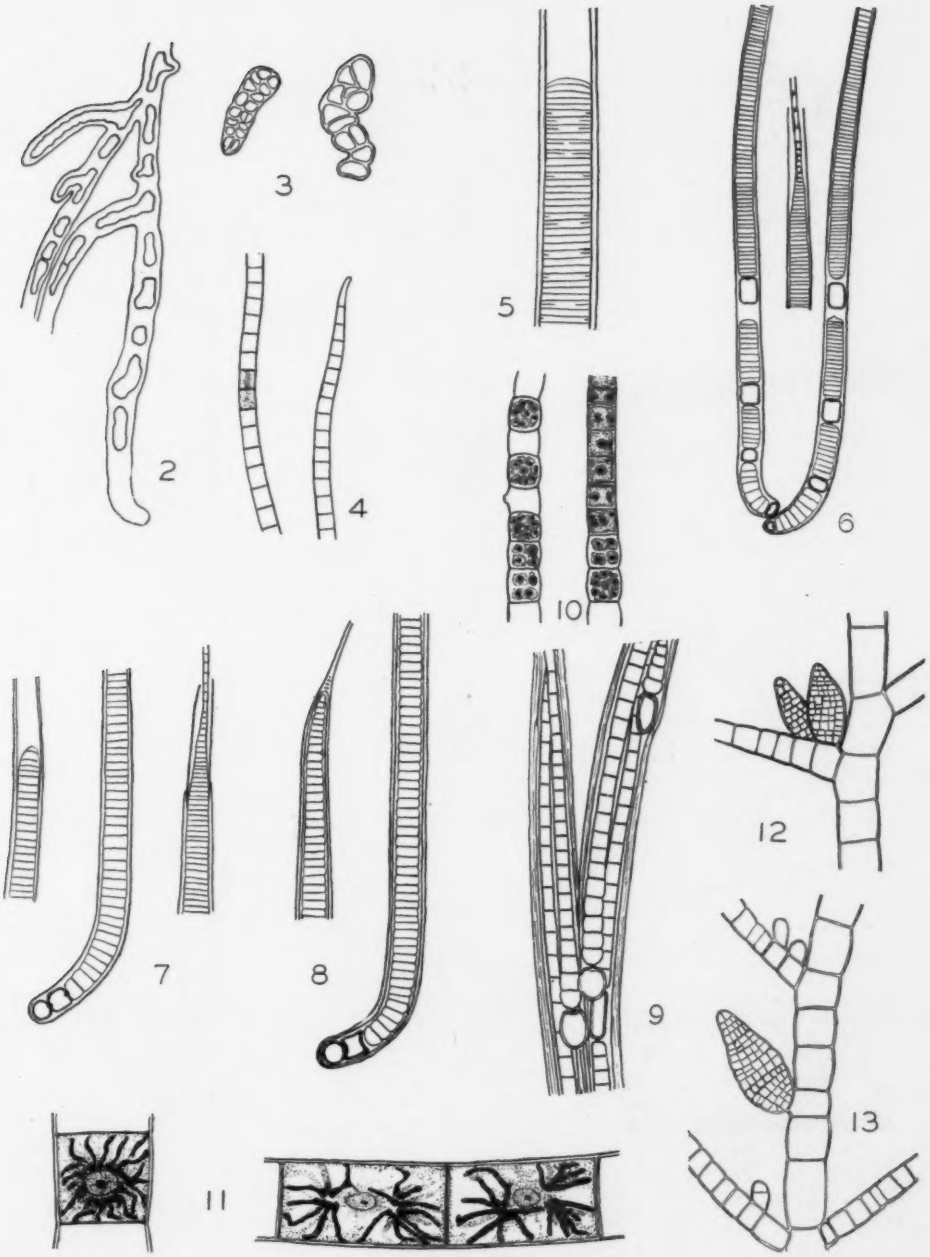

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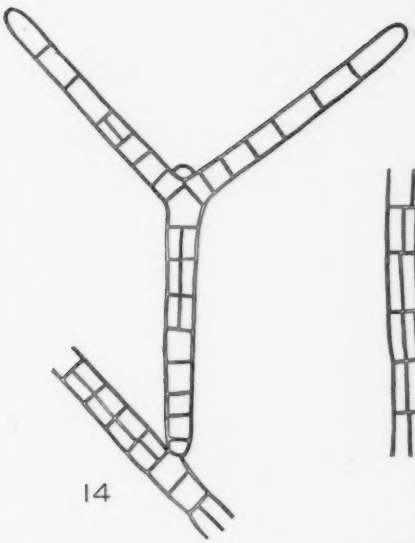
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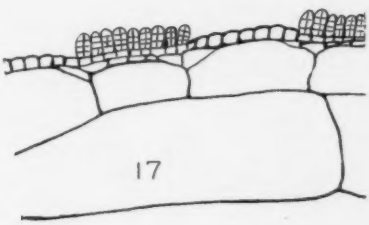
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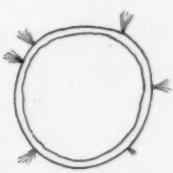
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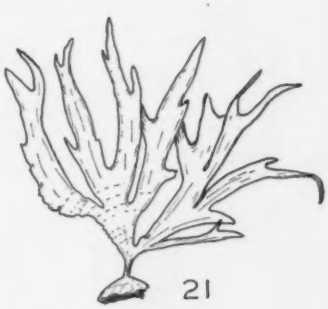
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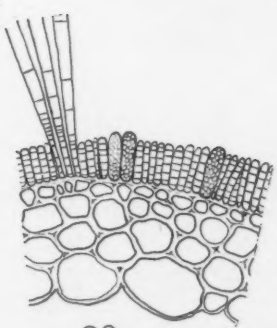
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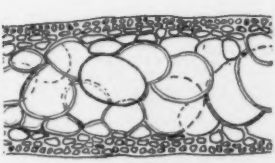
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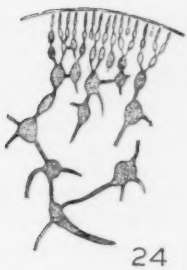
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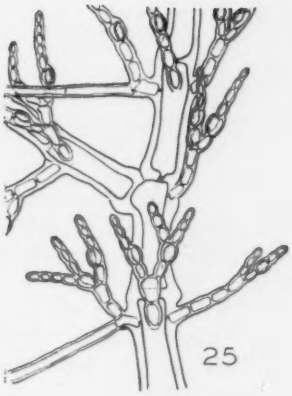
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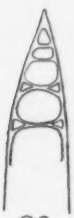
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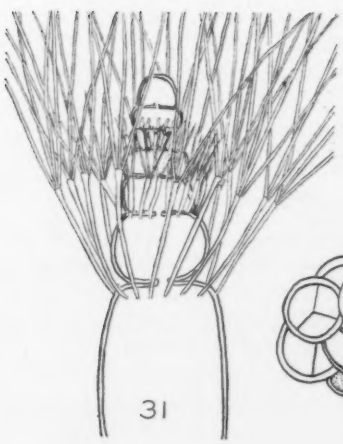
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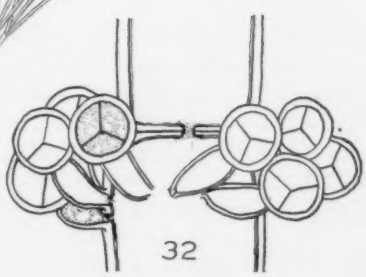
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THE SYMBIOTIC UTILIZATION OF CELLULOSE

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The abundant occurrence of cellulose, coupled with its potentialities as a source of glucose, makes it one of the most important of the polysaccharides. From a nutritional standpoint it is of interest because of the special problems involved in its utilization.

With a few exceptions (Karrer, 1930) microorganisms are the agents which decompose the major part of the naturally occurring cellulose. Great quantities are dissimilated by fungi, actinomycetes, molds, bacteria, and protozoa. In most instances in which higher animals utilize cellulose, the primary digestion is accomplished by microorganisms and the host benefits from the cellulose chiefly as a result of their activity. The host often develops special adaptations for harboring the microbes and furthering their development. This leads to a true symbiotic association from which both partners derive benefit. The microorganisms may become restricted in habitat to one or a few host forms and lose the ability to survive independently.

The best known examples of the symbiotic utilization of cellulose are found in termites and in ruminants. Both these host groups are of great economic importance. Their utilization of cellulose has been studied more than that of other forms such as horses (Choukevitch, 1911), rodents (von Tappeiner, 1883), and certain beetles (Wiedemann, 1930; Werner, 1926), which also display a symbiosis in the use of cellulose.

The present paper is an attempt to trace the solution of the various problems encountered in the study of the symbiotic utilization of cellulose by termites and ruminants and to summarize the evidence which supports the hypothesis that the primary conversion in the symbiotic utilization of cellulose is a typical fermentation by the microbial partner.

I. THE ESTABLISHMENT OF THE FACT OF CELLULOSE DIGESTION

One of the first problems was to demonstrate conclusively that a digestion of cellulose actually took place. This was early determined in the case of ruminants as a result of controlled feeding experiments in which the food and excreta were analyzed (Haubner, 1855; Henneberg and Stohmann, 1864). The results left no doubt but that a substantial part of the cellulose disappeared during passage through the ruminant and that nutritionally this digested cellulose was approximately equivalent to starch.

Cellulose digestion in the horse was also established (Ellenberger, 1879) though the efficiency of the utilization was somewhat less than that in ruminants (Zuntz, 1891). Ustjanzew (1905) showed that cellulose digestion occurred in the rabbit. Werner (1926) demonstrated it in a beetle.

The utilization of cellulose by termites was first definitely established by the analyses of Oshima (1919), though the excellent growth of termites on cellulose substrates had led earlier investigators to assume that it was utilized (Escherich, 1908).

II. THE IDENTIFICATION OF THE CELLULOSE-DIGESTING AGENTS IN THE RUMEN

The most significant early investigations aimed at identifying the agents responsible for cellulose digestion in cattle were those of von Tappeiner (1883, 1884, 1888). Indeed, these studies constitute one of the most important contributions to our knowledge of the mechanism of cellulose utilization in cattle. Von Tappeiner proved the symbiotic nature of the process by demonstrating cellulose digestion in *in vitro* cultures of the rumen contents. Extracts of the bovine tissues were completely inactive. Von Tappeiner ascribed the cellulose digestion to microorganisms but made no attempt to identify the responsible species.

Following von Tappeiner's work the importance of the rumen protozoa in cellulose digestion was considered and has been actively debated during much of the subsequent time. Some investigators came to the conclusion that the protozoa were unable to digest cellulose, whereas others, on the basis of comparable experiments, were convinced that the protozoa were of importance in this respect. Several techniques were used in studying this problem. Trier (1926) removed rumen contents to a flask and observed the ingestion of cellulosic plant parts by *Diplodinium*. He reported an increase in reserve food (glycogen) when cellulose was fed to the protozoa in the flask culture. Weineck (1934) reported that histochemical tests showed glucose present in the cytoplasm around ingested cellulose particles, a result indicating that the latter were digested. However, Usuelli (1930) and Westphal (1934, 1934a) in culture experiments similar to those of Trier came to the opposite conclusion, namely, that the protozoa were unable to digest cellulose.

These experiments were handicapped by inability to grow the protozoa *in vitro* and by the fact that the various investigators studied different organisms. The development of a culture method by Margolin (1930) overcame the first of these difficulties but his cultures contained a mixed fauna and aside from microscopic observation as practiced by previous workers, no technique was available for testing cellulose digestion.

The author grew single species of the rumen protozoa (1942, 1943) in sufficient numbers so that they could be tested directly for the enzyme cellulase. Extracts of the various species of *Diplodinium* showed an active cellulase which could be accounted for only on the supposition that it was produced within the protozoan. The possibility that the demonstrated enzyme was due to bacteria was eliminated by the use of suitable control experiments. Trier's observations on the synthesis of glycogen from cellulose by *Diplodinium* were fully substantiated when it was demonstrated that individuals of *D. maggii*, rendered glycogen free by starvation, showed definite glycogen deposits within one hour after the ingestion of cellulose.

In the same series of experiments which showed cellulase in *Diplodinium*, it could not be demonstrated in *Entodinium*. *Entodinium* did not grow on cellulose but became abundant when starch was supplied. It thus appears that the various rumen protozoa differ in their capacity to digest cellulose. This explains in part the conflicting results obtained by previous investigators. The species of *Diplodinium*, and related forms which ingest large plant parts, are active in cellulose digestion and thus are symbionts whereas the remaining protozoa are not directly concerned.

The question of the importance of the protozoa in cellulose utilization by the ruminant has been investigated experimentally by Becker, Schulz, and Emmerson (1929) and by Winogradowa, Winogradowa-Fedorowa, and Wereninow (1930). Both groups used a defaunation technique, the approach to the problem being comparable to that which was so fruitful in the study of the termite protozoa by Cleveland (1924). The rumen protozoa were killed by starvation and feeding suitable quantities of copper sulphate. The utilization of cellulose in these defaunated animals was compared with that occurring in the same animals with their normal fauna. No significant differences between the faunated and defaunated animals could be detected, suggesting that the protozoa were unable to digest cellulose. However, in view of the subsequent demonstration (see above) that certain of the protozoa do digest cellulose other explanations of the above results may be suggested: (1) the cellulose-digesting protozoa were few in number and quantitatively of no significance, and/or (2) when the protozoa were removed other agents took over the entire function of cellulose digestion.

In some cases the first explanation applies. It may be found, on microscopic examination of rumen contents, that *Diplodinium* and the other cellulose-digesting protozoa are relatively few in number. *Isotricha* and *Entodinium* predominate. Elimination of the protozoa from such a rumen would not noticeably affect cellulose digestion. On the other hand, many rumina contain large and significant numbers of *Diplodinium*. It is highly probable that the cellulose which they digest constitutes an appreciable part of the total. If such animals, when defaunated, show no impairment in cellulose utilization, it must be supposed that the second explanation applies, namely, that other organisms take over the entire function. In view of the established importance of bacteria as agents of cellulose digestion and their demonstration in the rumen (see below) it may be assumed that they are the responsible agents in the defaunated ruminant. In this connection it is significant that in the experiments of Becker et al. three weeks elapsed between defaunation and feeding of the experimental ration. This allowed ample time for establishment of a full bacterial flora.

There have been relatively few fruitful investigations on the isolation and identification of the bacteria concerned with cellulose digestion in the ruminant. Ankersmit (1905) attempted to grow cellulose bacteria using the methods of Omeliansky (1902) and inoculating with various amounts of rumen contents. He found spore-forming cellulose-digesting bacteria similar to those described by Omeliansky but they were not present in significantly large numbers and occurred in hay to the same extent as in the rumen. He concluded that the cellulose bacteria growing in his cultures were unimportant in the rumen.

Henneberg (1922) recognized the difficulties in culturing the cellulose bacteria of the rumen and utilized direct microscopic examination as a means of identifying them. Bacteria which were attached to the walls of plant cells and which appeared to have digested a portion of the wall, causing pits and depressions corresponding approximately to the shape of the bacteria, were considered as attacking cellulose. By this technique it was concluded that the most important cellulose-digesting bacterium in the rumen was a small spherical organism, *Micrococcus ruminantium*.

The author has developed a technique for culturing cellulose-digesting anaerobes (1944), and has applied it to the problem of culturing and identifying the cellulose-digesting bacteria in the rumen. It has been possible to demonstrate them (1946a) in numbers ranging from 18,000 to over 1 billion per ml. By using special care in fishing colonies, pure cultures of a number of strains have been obtained. The isolated organisms, and also those cellulose digesters from the rumen which have been observed microscopically in mixed cultures, appear to belong to two distinct types. One is a gram negative streptococcus which ferments cellulose relatively slowly in pure culture. The other is an irregular rod which is extremely active in cellulose decomposition. The latter appears to be quantitatively of more importance in the rumen samples which have thus far been studied.

The great numbers in which these bacteria occur and the rapidity with which they digest cellulose indicate that they play an important rôle in the rumen.

III. THE IDENTIFICATION OF THE CELLULOSE-DIGESTING AGENTS IN TERMITES

Several entomologists (Escherich, 1908; Imms, 1919) suggested that the protozoa in termites were the agents responsible for cellulose digestion in these insects. The first experimental evidence for this view was obtained by Cleveland (1923, 1924, 1925). A study of the food habits and intestinal fauna of various species and castes of termites showed a close correlation between the wood-eating habit and the presence of large numbers of flagellates in the gut. Defaunation of individuals caused loss of ability to use wood as food, but this capacity was recovered upon refaunation. By selective defaunation techniques, termites containing only one or two species of protozoa were obtained and in this way the cellulose-digesting ability of each species could be determined. *Trichomonas termopsidis* and all the large hypermastigote flagellates in *Zootermopsis* digested cellulose whereas the others did not. Subsequently, Trager (1932, 1934) demonstrated a cellulase in extracts of these protozoa.

The symbiotic cellulose-digesting protozoa in termites constitute an evolutionary series in the flagellates which parallels that of the ciliates in the rumen. In each group a large and remarkably complex morphological type has arisen. Both groups feed chiefly upon cellulose, and their habitat has become restricted to the alimentary tract of the host.

Because of the widespread activity of bacteria in cellulose digestion, culture tests for cellulose-digesting bacteria in termites have been made (Dickman, 1931; Beckwith and Rose, 1929; Hungate, 1936). These have used the ali-

mentary tract of *Zootermopsis* or *Reticulitermes* as inoculum. They have been uniformly unsuccessful in demonstrating any significant numbers of cellulose bacteria. Microscopic examination of the alimentary tract of *Zootermopsis* also indicates that bacteria are relatively unimportant in cellulose digestion. These termites are classed in the families *Kalotermitidae* and *Rhinotermitidae*.

The studies of Cleveland (1923) on the family *Termitidae* showed that the termites in this family did not contain protozoa, nor did most of them feed on wood. During his observations there were found no exceptions to the generalization that in termites the cellulose-digesting agents were protozoa. However, *Eutermes exitiosus*, a member of the *Termitidae*, is extremely destructive of wood in Australia, yet contains no protozoa. Holdaway (1933) reports that bacteria are numerous in the alimentary tract of this form and it is highly probable that active digesters of cellulose are included among them. The author has collected another member of this family, *Amitermes minimus*, in oak wood and has maintained the colony for 18 months in the laboratory with only the wood as food. Microscopic examination of the gut contents showed large numbers of actively motile bacteria. Two anaerobic cellulose-digesting microorganisms were isolated from this termite: *Clostridium* sp., and *Micromonospora propionici* (Hungate, 1946). It is highly probable that cellulose digestion in other wood-eating species of the *Termitidae* will be found to be accomplished by bacteria.

In the termites that have been studied, no examples showing significant cellulose digestion by both bacteria and protozoa have been found. The relatively long survival of wood-fed defaunated *Kalotermes tabogae* and *Neotermes holmgreni* (Cleveland, 1928) suggests the possibility of both bacterial and protozoan digestion in these forms.

IV. THE MECHANISM OF THE SYMBIOSIS IN TERMITES

One of the first explanations of the symbiosis between the termite and its cellulose-digesting protozoa was that the protozoa formed sugar which was absorbed by the host (Cleveland, 1924). This assumed that glucose was excreted from the protozoa as the chief product from their utilization of cellulose and that it was absorbed and metabolized by the insect host, presumably undergoing oxidation to carbon dioxide and water.

Conclusive evidence that glucose was formed from cellulose by the termite protozoa was obtained by Trager (1932), using an extract of the protozoa. The question then arose: Was glucose a final product of cellulose utilization by the protozoa, or was it an intermediate which was in turn converted to other materials? Trager (1934) succeeded in culturing *Trichomonas termopsidis* on cellulose and tested for sugar in the culture medium. Although unable to demonstrate glucose chemically, its production in minute quantities was inferred from the fact that an accompanying bacterium produced gas in the mixed cultures. Pure cultures of the bacterium produced gas from glucose but not from any of the other substrates which were tested.

There are several difficulties in accepting the hypothesis that glucose is the material given off by the protozoa and absorbed by the termite. It has not been

possible to demonstrate glucose in the gut contents of the termite or in cultures of the protozoa (Hungate, 1943a). Furthermore, the scheme does not provide a source of energy for the protozoa, since the digestion of cellulose to glucose is a hydrolytic reaction with little accompanying decrease in free energy. This difficulty may be avoided by assuming that part of the glucose is retained and metabolized by the protozoa whereas the rest is excreted and used by the termite. But in that case the excreted glucose should be chemically detectable, particularly in *in vitro* cultures. Its absence makes it very doubtful that any appreciable quantities of glucose are absorbed by the termite.

An alternative to the glucose theory of the mechanism of the symbiosis between the termite and its protozoa (Hungate, 1939) postulates that the glucose produced by the digestion of cellulose is retained within the bodies of the protozoa and undergoes a dissimilation which yields energy for their life processes. The protozoa digest the cellulose to glucose and utilize the latter as a source of energy. Three possible modes of this utilization may be proposed. (1) The protozoa might oxidize the glucose to carbon dioxide and water. The termite would not derive benefit from this process, and it could not, therefore, explain the symbiosis. (2) The protozoa might oxidize only a part of the glucose and excrete the rest. Under these circumstances the protozoa should be aerobic and glucose should be present in the gut contents. Neither of these has been demonstrated. (3) The protozoa might ferment the glucose under anaerobic conditions, giving off carbonaceous materials capable of further oxidation. These latter might be absorbed and utilized by the termite. Under such circumstances the protozoa and the termite would be partners in the total degradation of the cellulose. The protozoa would accomplish the initial digestion to glucose and the fermentation of the glucose. The termite would oxidize the fermentation products to carbon dioxide and water.

The original observations of Cleveland (1925) on the effectiveness of oxygen in killing the protozoa suggested that they were obligate anaerobes. In his *in vitro* cultures, Trager (1934) observed that growth took place under anaerobic conditions. The author (1939) tested the effect of oxygen on protozoa removed directly from the termite and also found them anaerobic.

Cook (1932) noted the production of an undetermined gas (not CO_2) by faunated *Zootermopsis* and Randall and Doody (1934) noted an odor suggestive of volatile acid when the gut contents were acidified. Both these observations suggested the presence of incompletely oxidized products such as are commonly produced in fermentations. Coupled with the obligate anaerobic habit of the protozoa, they strongly suggest that the latter meet their energy requirements by a typical fermentation.

The author used the Warburg technique to demonstrate the fermentative nature of the cellulose utilization by the termite protozoa (1939). A washed suspension of protozoa obtained directly from termites was shown to produce carbon dioxide, hydrogen, and acetic acid. Estimates of the amount of products formed indicated that they were of a magnitude capable of accounting for a large part of the cellulose digested in the termite.

The hypothesis that glucose is fermented by the termite protozoa is also supported by Cook's experiments (1943) in which glucose-fed faunated termites showed hydrogen production.

In another series of experiments (Hungate, 1943a) weighed quantities of cellulose were fermented by the protozoa of *Zootermopsis* and the products were measured. Two types of fermentation were encountered, one characterized by equal amounts of carbon dioxide and hydrogen, and relatively large amounts of acetic acid, the other by equal amounts of carbon dioxide and acetic acid and relatively large amounts of hydrogen.

Evidence of both these types of fermentation had previously been observed in studies on the respiration of normal faunated termites. One group of faunated termites consistently produced large quantities of hydrogen. This observation, coupled with Cook's (1932) demonstration that a gas other than carbon dioxide is produced by faunated termites, suggested that hydrogen was not utilized by the termite. Accordingly, the magnitude of its production could be used as an index of the amount of cellulose fermentation by the protozoa in the intact termite, assuming that the ratio between the hydrogen and the other products of the fermentation was the same in the intact termite as in the Warburg experiments.

In this way it was possible to estimate roughly the amount of acetic acid and other oxidizable products formed in the intact termite. The amount of oxygen required for the complete oxidation of these products was then calculated and compared with the oxygen consumption of the insect. These calculations indicated that the fermentation products were of sufficient magnitude that their oxidation would require an amount of oxygen approximately equal to that actually consumed by the faunated termite. This shows that the cellulose fermentation by the termite protozoa yields sufficient oxidizable products to meet the energy requirements of the host.

Another line of evidence in support of the glucose fermentation theory of the termite-protozoa symbiosis was obtained by testing the food (wood), hind-gut contents, and fecal pellets of *Zootermopsis* for acetic acid. It could be demonstrated in the gut contents but not in the wood or pellets. This is in agreement with the view that it is produced in the hind-gut and absorbed by the termite. It was also found that the wall of the hind-gut was permeable to acetic acid.

The question arises whether all the glucose formed by digestion of cellulose undergoes a fermentation by the protozoa. Although no conclusive evidence is available on this point several observations suggest that all the glucose is fermented. As noted previously, no glucose can be demonstrated in *in vitro* cultures. The over-all metabolism of the faunated termite is the complete oxidation of cellulose to carbon dioxide and water (with the exception that some hydrogen escapes oxidation). No significant quantities of soluble materials are excreted. The energy yield from the anaerobic fermentation of cellulose by the protozoa is small compared to the energy obtained by the termite upon subsequent oxidation. Yet the protozoa make up an appreciable fraction of the weight of the termite (Kirby, 1941) and they are extremely active. Therefore,

it seems highly probable that all of the glucose formed by the protozoa must be fermented by them to satisfy their energy requirements.

The above evidences support the hypothesis that the mechanism of cellulose utilization in the termite involves a primary cellulose fermentation by the protozoa and the absorption of the fermentation products and their oxidation by the termite. One important experimental result which would round out the evidence for the cellulose fermentation hypothesis is still lacking. If acetic acid is one of the chief materials produced by the protozoa and utilized by the termite, it should be possible to maintain defaunated termites for a considerable period on a diet of acetic acid. Cook (1943) has attempted this (feeding sodium acetate) and so has the author (feeding calcium acetate) but in neither case did the insects live significantly longer than wood-fed controls. These results indicate that acetate is not utilized by the defaunated termite. However, in view of the evidence that appreciable quantities of acetic acid are produced in the alimentary tract and are not found in the fecal pellets it seems inescapable that it must be absorbed and oxidized.

In the faunated termite there is a continuous and gradual production of free acetic acid. This may favor its absorption. Further studies will be necessary to resolve the discrepancy between the apparent production of acetic acid in the faunated termite and the apparent inability of the defaunated termite to utilize it.

V. THE MECHANISM OF THE SYMBIOSIS IN CATTLE

Ideas concerning the mechanism of the symbiotic cellulose utilization in cattle have undergone an interesting evolution, beginning with Haubner's demonstration of the digestibility of cellulose, and extending to the present time. Von Tappeiner's work showed clearly that microorganisms were responsible for the breakdown and that they accomplished an anaerobic fermentation. Volatile acids, carbon dioxide, and methane, were demonstrated as the final products. It was postulated that the volatile acids were absorbed and oxidized by the host. Several investigators tested to see if the volatile acids, principally acetic and butyric, were utilized by mammals.

Munk (1890) and Mallèvre (1891) showed that when salts of acetic and butyric acids were injected into the rabbit the anions were speedily utilized. The respiratory quotient was modified, due to carbon dioxide retention by the cations, and later the cations were eliminated in the urine. The acids were not excreted in any significant amounts. Wilsing (1885) found that the amount of volatile acid appearing in the excreta of the goat was small in comparison to the amount calculated to be produced in the rumen fermentation.

Boycott and Damant (1907) reported that if the respiratory quotient of the goat were corrected for the carbon dioxide production in the rumen, it was 0.85, a "figure which is not in accordance with the view that cellulose is dealt with by the tissues as a carbohydrate rather than as a fatty acid arising from the carbohydrate by bacterial action before assimilation."

These investigations supported the view that the cellulose utilization in the ruminant was accomplished via a preliminary fermentation by microorganisms in the rumen.

At the same time that the cellulose fermentation hypothesis was being developed by von Tappeiner and these other workers, the alternative theory of cellulose utilization through sugar was also considered. Knowledge of the mechanism of starch digestion in mammals apparently led Henneberg and Stohmann (1885) to postulate a similar mechanism to explain cellulose utilization in the ruminant. "Es scheint wenig wahrscheinlich, dass die ganz unlösliche Cellulose als solche, in ungelöstene Zustand, von den Gärungsorganismen angegriffenen werde, es ist nicht glaublich, dass die Bakterien Cellulose fressen. Viel wahrscheinlicher ist vielmehr die Annahme eines allerdings noch nicht bekannten, Uebergangsstadiums, welches zwischen der unlöslichen Cellulose und den Gärungsproducten liegt, in welchem die Cellulose in einer löslichen Körper verwandelt wird, der zu ihr in einem ähnlichen Verhältnis steht, wie die Maltose zu dem Stärkemehl. . . . Existiert aber ein solcher Körper und ist derselbe resorptionsfähig, so wird es fraglich, welcher Theil der Cellulose in dieser Form zur Resorption gelangt und wie viel davon für die Gärung ubrig bleibt." The subsequent demonstration of glucose as the product of cellulose hydrolysis gave credence to this idea.

Enzymes capable of splitting cellulose were discovered in barley seeds (Brown, 1892), in the snail (Biedermann and Moritz, 1898), and in a fungus found in the rumen (Ellenberger, 1915). More significant than any of these was Pringsheim's (1912) demonstration of cellulolytic enzymes in various cellulose cultures undergoing a bacterial fermentation. He proved the existence of a bacterial cellulase which split cellulose to cellobiose, and of a cellobiase which catalyzed the breakdown of cellobiose into two molecules of glucose. This established that the path of cellulose dissimilation included an intermediate sugar stage.

These experimental results supported the idea of direct absorption of glucose as the mechanism of symbiotic cellulose utilization. Relatively less attention was paid to the fermentation theory during the two subsequent decades, although Krogh and Schmidt-Jensen (1920) apparently accepted it in interpreting their work. The glucose view was adopted by Woodman and Stewart (1928) in explanation of the ruminant utilization of cellulose. It was also used by Cleveland to explain the mechanism of the symbiosis in the termite. The lack of knowledge and appreciation of the earlier fermentation view is reflected in the statement by Marston (1939): "If, as the existing experimental evidence implies, the ruminant derives practically all of its energy requirements from cellulose, and if the end products arising from bacterial cleavage of this material in the rumen are fatty acids, an extraordinary intermediate energy metabolism might be expected. Little or no reference is made in the literature to this interesting implication."

The author was led by the results of studies on cellulose fermentation in the termite, to postulate that a similar mechanism might occur in the ruminant. A study of the literature showed that this had been the original hypothesis stemming from the work of von Tappeiner and supported by the results of Munk, Mallèvre and Wilsing. The theory had been dropped later in favor of the glucose explanation and was only beginning to be revived (Woodman and Evans, 1938). After first upholding the glucose view the experimental results of

Woodman led him to adopt the fermentation theory, and at the present time this view is again being given serious consideration by investigators in this field. Briefly stated, it postulates, as in termites, that the glucose formed through cellulose digestion by the symbiotic microorganisms is fermented by them to yield energy and that the fermentation products are absorbed and utilized (at least in part) by the ruminant host.

The analysis of the exact mechanism of cellulose utilization in the ruminant is complicated by the fact that so many kinds of organisms are present. Estimates of the kind and amount of substrates used and products formed by the different microorganisms are needed. This analysis involves the separation of the various species, a study of their metabolism, and controlled tests of their interactions. Although work along this line has barely started, a few pertinent results have accumulated.

TABLE 1

Results of manometric studies on Diplodinium

EXPT.	PROTOZOAN	PRODUCTS		
		CO_2 $\frac{(\text{mmols})}{100}$	H_2 $\frac{(\text{mmols})}{100}$	Acid $\frac{(\text{millieq.})}{100}$
1	*D. neglectum*	0.05	0.12	0.13
2	"	0.37	0.21	0.55
3	"	0.21	0.42	0.93
4	"	0.72	0.49	0.63
5	*D. maggii*	0.24	0.23	0.31

The mechanism of the cellulose utilization by the cattle protozoa (*Diplodinium*) involves a preliminary split to cellobiose and to glucose (Hungate, 1942). This is accomplished by intracellular enzymes. The protozoa are obligate anaerobes and must therefore meet their energy requirements by fermenting at least part of the glucose formed. Evidence that they do accomplish an anerobic fermentation has been obtained in manometric experiments using washed suspensions of the protozoa. The latter were obtained from clone cultures grown on grass and cellulose. Carbon dioxide, hydrogen (determined by absorption with palladium black), and acid were found to be produced. A summary of the experiments is given in table 1.

In experiment 4 a control was run using the debris in the washings from the protozoa. It showed a negligible production of fermentation products. In other experiments the debris was found to show a higher fermentation rate which was still considerably below that exhibited by the suspension of *Diplodinium*.

A steam distillation for volatile acid was run on experiment 5. Volatile acid was found to be present in amounts approximately equal to the total acid. The identity of the acid was not established.

A preliminary manometric experiment using *Isotricha* obtained directly from the rumen showed that these protozoa also produce hydrogen, though in this genus material other than cellulose is fermented.

These experiments show clearly that the rumen protozoa obtain their necessary energy by a fermentative conversion of the substrate. In the case of *Diplodinium* this substrate is chiefly cellulose or the glycogen derived from it. These findings are in agreement with the hypothesis that the mechanism of cellulose utilization in the ruminant is through a preliminary microbial fermentation.

The question arises whether all of the glucose formed by *Diplodinium* from cellulose undergoes a fermentative dissimilation or whether part of it may be excreted and be absorbed directly by the host. Species of *Diplodinium* are apparently able to split more cellulose than is required for their immediate needs, since a deposition of glycogen occurs when an abundance of cellulose is present. However, it is questionable whether any glucose is excreted and even if it were to escape from the bodies of the protozoa it is doubtful whether any would be absorbed by the host. Other microorganisms in the rumen fluid would quickly use it.

The requirements of *Diplodinium* for utilizable substrate are probably quite high, as evidenced by the rapidity with which reserve glycogen is depleted during starvation. The rapid conversion of cellulose to fermentation products increases the utility to the host.

The available evidence indicates that the bacterial conversion of cellulose in the rumen also includes a fermentative dissimilation. The exact nature of the products has not yet been determined but observations on the pure cultures grown in shake tubes indicate that relatively little gas is formed. However, there is a marked production of acid. It is highly probable that the bacteria ferment all of the cellulose which is digested. Glucose and cellobiose are rapidly attacked.

The cellulose bacteria which have been cultured from the rumen show less tendency for production of an extracellular cellulase than has been observed in most other anaerobic cellulose-digesting bacteria. Colonies of the streptococcus show a small area around the colony in which the cellulose has been digested but in which there are no bacteria. However, the extent of this cleared area is much less than is observed with *Clostridium cellobioparus* (Hungate, 1944) and *Micromonospora propionici* (Hungate, 1946).

The rod-shaped cellulose bacterium from the rumen has shown no indications of an extracellular cellulase. The cellulose is digested only in the immediate vicinity of the colony and the clearing of the cellulose takes place only as fast as the bacteria migrate through the agar. Old tubes containing dead bacteria show no further cellulose digestion upon continued incubation, in contrast with the results obtained with most other forms. In this respect these cellulose bacteria resemble the cellulose-decomposing myxobacteria (Stanier, 1942) in which it has not been possible to demonstrate an extracellular cellulase.

The apparent lack of an extracellular cellulase in this most important cellulose bacterium in the rumen makes it doubtful whether much of the cellulose utilized by them is given off in the form of glucose. It is highly probable that the

primary conversion of cellulose by the rumen bacteria includes a fermentation which supplies them with their necessary energy.

VI. A COMPARISON OF THE MECHANISM OF THE SYMBIOSIS IN TERMITES WITH THAT IN CATTLE

The results reported thus far suggest a similarity between the mechanism of cellulose utilization in the termite and in the ruminant. However, there are a few differences which may be considered. There is little evidence of growth of the protozoa in the termite gut during the interval between molts. Andrew and Light (1929) have shown that mitoses are extremely rare. Following ecdysis there is a rapid multiplication of the individuals which gain access to the gut but once the normal fauna is established further divisions cease. It is thus apparent that during most of the instar the host derives little food through digestion of the bodies of the protozoa.

In the rumen, on the other hand, there is a continuous growth of the bacteria and protozoa with the consequence that large numbers of them pass on into the adjacent portions of the stomach and are digested. The importance of this in ruminant nutrition is suggested by the experiments on the utilization of simple forms of nitrogen by cattle (Hart, Bohstedt, Deobald, and Wegner, 1938). Urea and ammonium carbonate, fed in amounts such that they constituted about 70 per cent of the total nitrogen in the diet, supported as rapid growth as was obtained with casein. The mechanism of this utilization of simple nitrogen is undoubtedly through a synthesis of microbial protoplasm by the rumen organisms and digestion of their bodies by the host. Synthesis of vitamins in the rumen may be similarly explained.

The symbiotic utilization of cellulose in termites and in cattle involves the elimination of certain fermentation products which cannot be used by the host. In termites, hydrogen constitutes this unutilizable material. In ruminants, it is methane; no hydrogen is given off (Lugg, 1938).

The hydrogen production by the faunated termite is readily explained by its occurrence as one of the products of the primary cellulose fermentation. Thus far there is no evidence that methane is produced in the rumen during the primary fermentation of cellulose by either the protozoa or the bacteria. A few of the shake tubes containing pure cultures of the cellulose bacteria from the rumen have shown gas splits in the tube, but upon analysis by combustion methods hydrogen has been found to be the only combustible gas present. No direct tests for methane production by the cattle protozoa have been made, but the presence of hydrogen makes it doubtful whether any methane was simultaneously produced, since these two gases are not known to occur together as fermentation products of a single species.

These observations suggest that the methane production in the rumen is due to a secondary flora which utilizes the primary products of the cellulose fermentation and transforms them into other materials, including methane. In view of the fact that hydrogen is produced in the primary cellulose fermentation but is absent from the final products, it is tempting to suggest that it is utilized in the

production of the methane. A reduction of carbon dioxide to methane with molecular hydrogen has been shown to be accomplished by *Methanobacterium omelianskii* (Barker, 1943).

Some evidence that a mixed flora is concerned with the production of methane has been obtained. In the shake tube series for cellulose bacteria inoculated directly with rumen contents, gas splits were common and methane could be shown to be formed. If a large inoculum was transferred from one of these tubes of lower dilution, methane was found in the subsequent series. But if a single cellulose-digesting colony from a tube of higher dilution was transferred, there was a marked decrease in gas production and after pure cultures were obtained no traces of methane could be demonstrated.

It might be postulated that the methane production was due to a cellulose bacterium present in fewer numbers than the cellulose decomposers which were obtained from the tubes of higher dilution. However, the working hypothesis that methane is due to a secondary flora appears more attractive.

In addition to the methane production, there are undoubtedly other secondary reactions occurring within the rumen, accomplished by one or another of the many microorganisms present. The fermentation products initially formed by the cellulose bacteria and protozoa may undergo further anaerobic transformations before they are absorbed by the host.

VII. THE GENERAL APPLICABILITY OF THE CELLULOSE FERMENTATION HYPOTHESIS

Although the microorganisms associated with the cellulose decomposition in horses, rodents, and insects other than termites have not been investigated in as much detail as those in ruminants and termites, the data which are available are in agreement with the hypothesis that an anaerobic fermentation of the cellulose is the first step in its utilization. The caecum of the horse and that of the rodent are completely anaerobic and the energy requirements of the microorganisms must be met by a fermentative dissimilation of the substrate.

It seems justifiable to extend to these other forms the hypothesis of an initial anaerobic cellulose fermentation as the mechanism of the symbiotic utilization of cellulose. The validity of this extension can only be determined by further experimental studies. It is to be hoped that the presentation of the cellulose fermentation theory will stimulate investigations leading to a more complete understanding of the mechanisms underlying each of the examples of symbiotic cellulose utilization found in nature.

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ANTHRACNOSE OF DWARF MISTLETOE CAUSED BY A NEW SPECIES OF SEPTOGLOEUM*

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Plates 4–6 and 4 Text Figures

INTRODUCTION

The dwarf mistletoes, *Arceuthobium* spp., are exceedingly important parasites of conifers in North America. They cause extensive damage in western forests, ranking next to heart rots in the losses produced, and in the future, on cut-over forest areas, will probably be far more damaging than fungi unless more attention is given to their control (Boyce, 1938: 352). The most efficacious means now known for controlling this serious phanerogamic parasite consists of the careful and repeated pruning out of infected branches and the removal of severely affected trees from the stand (Perry, 1922; Weir, 1923), but this is an arduous and costly task. A destructive disease of *Arceuthobium* has been found which is of particular interest because it is a striking example of a parasite attacking another important parasite and because the causal organism, a hitherto undescribed fungus, apparently offers some promise as an agent of biological control.

The dwarf mistletoes have only a few natural enemies. Bark-eating rodents sometimes cut off twigs bearing mistletoe infections, and spittle insects (Cercopidae) often mine out and kill shoots of *A. vaginatum* (Willd.) Presl. and *A. campylopodum* Engelm. (Gill, 1935: 221). Weir (1915) noted that grasshoppers eat mistletoe shoots and seem to prefer the staminate ones. Two fungi, *Wallrothiella arceuthobii* Peck and *Metasphaeria Wheeleri* Linder, have previously been reported on *Arceuthobium*. The parasitism of the former is well known from the works of Peck (1875), Wheeler (1900), Weir (1915), and Dowding (1931). It is rather widely distributed, having been reported from Arizona, Idaho, Michigan, Montana, and New York, and from Alberta and Manitoba, Canada. *Metasphaeria Wheeleri*, however, is apparently limited in distribution, having been reported only on *A. campylopodum* from one locality in California (Linder, 1938).

In 1935 Gill (1935: 220) gave a brief account of an apparently parasitic imperfect fungus associated with the premature death of shoots of certain forms of *A. campylopodum* in Washington and Arizona. The writer (1939) gave a further account of the distribution of this disease together with brief descriptions of symptoms and the associated fungus. Later (Bur. of Pl. Ind. 1940) attention was again called to the disease and to the possibility of employing the fungus as

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an agent of biological control against mistletoe in recreation areas and certain administrative forest sites where pruning and cutting are especially undesirable. Subsequent investigations have established the identity and pathogenicity of the associated fungus and the present paper gives a more comprehensive account of the disease and of the characteristics and behavior of the causal organism.

The major portion of the field and laboratory studies were performed during 1938, 1939, and 1940, while the writer was engaged in making mistletoe surveys in Arizona and New Mexico for the Division of Forest Pathology, U. S. Department of Agriculture, with headquarters at Albuquerque. Additional field work was carried out in that area during September, 1944. Further laboratory studies and other phases of the investigation were conducted at the University of North Carolina, at intervals from 1941 to the present time.

The writer is especially indebted to Dr. L. S. Gill for guidance and suggestions on phases of the study conducted in the Southwest. Grateful acknowledgement is also made to Dr. J. N. Couch, Dr. C. W. Edgerton, Dr. S. G. Lehman, Dr. D. L. Linder, and Dr. F. A. Wolf for advice on mycological questions, to Dr. Thomas Kerr for assistance in obtaining photomicrographs, to Miss Edith K. Cash for preparation of the Latin description, and to Dr. J. H. Jensen for helpful suggestions on the preparation of the manuscript.

THE HOST

Since the fungus disease under consideration affects a host plant which is in turn also a parasite with more or less exacting requirements, a brief account of its distribution and behavior is desirable.

The dwarf mistletoes are dioecious flowering plants of the family Loranthaceae. They are restricted to the Pinaceae and have been reported only in the northern hemisphere. According to Gill's (1935) monograph of *Arceuthobium* in the United States, five of the eight species now recognized occur in this country. Only one, *A. pusillum* Peck on species of *Picea* and *Larix* and once reported on *Pinus strobus* L. (House, 1935), occurs in the Eastern United States. The other four, *A. americanum* Nutt. and *A. vaginatum* (Willd.) Presl. on *Pinus* spp., *A. douglasii* Engelm. on *Pseudotsuga taxifolia* (Lamarck) Britt., and the eight forms of *A. campylopodum* Engelm. on species of *Abies*, *Larix*, *Picea*, *Pinus*, and *Tsuga*, occur in Western States. The other three species, *A. chinense* Lec. on *Abies* sp., *A. minutissimum* Hooker on *Pinus excelsa* Wallich and *A. oxycedri* (DC.) M. Bieb. on various Cupressae, are known only on the Eurasian continent.

The mistletoe plant forms an extensive haustorial system in the cortex of the host and puts out prennial, aerial, jointed shoots on which the floral parts are borne. The shoots of *A. pusillum* and *A. douglasii* are less than 35 mm. long and seldom more than 1 mm. in diameter, while those of *A. campylopodum* and *A. vaginatum* range from 20 to 150 mm. long and are 2 mm., or more, in diameter. The leaves are reduced to opposite pairs of tiny scales at the top of each segment. The pistillate flowers are two-parted and sessile, while the staminate ones are typically three-parted and sessile, except in *A. americanum* in which they are borne on pedicle-like segments. The fruits or berries each contain one seed

embedded in a mucilaginous pulp. At maturity these seeds are forcibly ejected and adhere to objects with which they come in contact. On germination the radicle forms a holdfast from which the primary haustorium develops and penetrates the young bark of the host. Penetration occurs only through bark less than three years old.

The aerial parts contain some chlorophyll, but the plant takes most of its required elaborated food from its host. Cannon (1901: 388) believes that *Arceuthobium* is a total parasite, and Dufrenoy (1936) contends that active translocation of nutrients occurs between the rays of the host and the haustoria of the parasite. The most striking symptom of mistletoe infection on the tree is the formation of witches' brooms. The general effect on the host is a marked reduction in rate of growth, and vigor may ultimately be reduced to such an extent that death results. Trees of all ages are affected.

DESCRIPTION OF THE DISEASE

Anthracnose affects primarily the stems of *Arceuthobium*, although infections have frequently been observed on the fruits. In the early stages the disease is characterized by the production of small, yellowish-white lesions along the stem. These gradually enlarge, coalesce, and erupt irregularly through the cuticularized epidermal layer disclosing conspicuous white spore masses (Pl. 4). Lesions occur in abundance on all parts of the stem but most commonly originate at or near the nodes. Basal lesions, which originate at the point where the stem issues from the bark, are also common.

The first indication of the disease to be noted in the field is usually the death of large numbers of shoots, and, in areas where it is well established, the low ratio of pistillate to staminate plants. Upon closer examination the most conspicuous sign of the disease is the presence of the white spore masses along the ruptured stems. These are most striking on plants which have just succumbed and on still living plants in which the disease is well advanced. Still closer examination reveals an abundance of the smaller, yellowish-white lesions still covered by the epidermal layer, ranging in size from barely visible spots up to 2 mm. in diameter. Several lesions may converge so that often the major portion of the stem is involved (Pl. 4, fig. 2 a and c). Death due to the disease may occur at any season of the year but is most common during the summer and fall. In collections made during April and May the majority of the lesions were small and covered. From June through September erupting stages were common and large numbers of shoots had been killed, while in the late fall and winter the disease was usually evident only on plants already dead. Shoots may be affected at all stages of development. The disease has been observed on tiny young shoots only recently emerged from the bark of the host as well as on large plants which have flowered one or more times.

Pistillate plants are more frequently attacked than staminate ones. Gill (1935: 220), in describing the disease on *A. campylopodum* forma *tsugensis* near Longmire, Washington, noted that, although staminate plants were common, pistillate plants bearing fruits were extremely rare. The writer has noted similar

situations in connection with the disease, especially on *A. campylopodum* forma *cyanocarpum* and forma *microcarpum*. On these hosts in the Graham Mountains in Arizona in September, 1944, it was not uncommon to observe heavily mistletoe-infected saplings on which only staminate plants could be found. Limited counts on *A. campylopodum* forma *cyanocarpum*, in localized areas in both the Graham and Santa Catalina Mountains where the disease is severe, showed living staminate plants outnumbering pistillate ones in ratios ranging from 2:1 to as much as 20:1. This apparent affinity on the part of the parasite for pistillate plants is of considerable importance in limiting the reproduction and spread of mistletoe. However, the disease is not confined to pistillate plants. Careful observation usually revealed a number of infected staminate plants in all areas where the writer has collected the disease. Differences in the susceptibility of pistillate and staminate plants of dioecious species to attacks by parasitic fungi have previously been noted. *Wallrothiella arceuthobii* attacks only pistillate plants of *Arceuthobium*. Clinton and McCormick (1924) discovered that pistillate plants of *Ribes alpinum* L. were susceptible to white pine blister rust (*Cronartium ribicola* Fischer) while staminate ones were immune to both this rust and *C. occidentale* Hedgc., Bethel and Hunt. Their work was corroborated and further emphasized by Hahn (1939, 1941).

Minor symptomatic variations are exhibited by certain of the host species and forms. Nodal lesions are particularly frequent on *A. campylopodum* forma *tsugensis* and on this host appear to originate almost exclusively at that point (Pl. 4, fig. 2b). On *A. campylopodum* forma *divaricatum* and on *A. douglasii* the fruiting bodies remain covered by the epidermal layer somewhat longer than on other hosts, so that the erupting white spore-mass stages are less frequently encountered. The affinity of the fungus for pistillate plants is also less pronounced on *A. douglasii*, and on this plant the disease is apparently not as widespread or severe as on other hosts. The latter impression may be attributed in part to the fact that this plant is relatively much smaller and less conspicuous than other western species.

HOST RANGE AND DISTRIBUTION

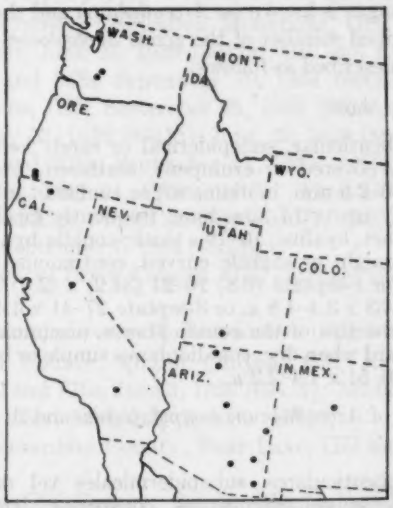
Anthracnose of dwarf mistletoe has a rather wide geographical distribution, having been found to date in six western states: Arizona, California, New Mexico, Oregon, Utah, and Washington (Text fig. 1). In addition to numerous known collections of the disease itself, it was found by the writer on a number of herbarium specimens of the host taken by collectors working in western forests over a period of several years. It has been observed in nature on seven of the eight forms of *A. campylopodum* and on *A. douglasii*. The fungus also parasitizes *A. vaginatum* forma *cryptopodum* following artificial wound inoculations but has not been observed on this species in nature. In the following list, which gives the species and forms of *Arceuthobium* on which the disease has been found, together with the host range of each mistletoe (as based on Gill, 1935), the asterisk (*) designates tree species from which anthracnose-infected mistletoe has been collected.

Arceuthobium campylopodum forma *abietinum* (Engelm.) Gill: *Abies amabilis* (Loudon) Forbes*, *A. arizonica* Merriam, *A. concolor* Lindley and Gordon*, *A. grandis* Lindley, *A. lasiocarpa* (Hooker) Nuttall, *A. magnifica* A. Murray*, *A. nobilis* Lindley:

A. campylopodum forma *blumeri* (A. Nelson) Gill: *Pinus lambertiana* Douglas, *P. monticola* D. Don, *P. strobiformis* Engelm.*:

A. campylopodum forma *cyanocarpum* (A. Nelson) Gill: *Pinus albicaulis* Engelm., *P. aristata* Engelm., *P. flexilis* James*:

A. campylopodum forma *divaricatum* (Engelm.) Gill: *Pinus cembroides* Zuccarini, *P. edulis* Engelm.*, *P. monophylla* Torrey and Fremont*:



TEXT FIG. 1. GEOGRAPHICAL DISTRIBUTION OF THE ANTHRACNOSE DISEASE OF DWARF MISTLETOE

A. campylopodum forma *microcarpum* (Engelm.) Gill: *Picea breweriana* S. Watson, *P. engelmannii* Engelm.*, *P. pungens* Engelm.:

A. campylopodum forma *tsugensis* (Rosendahl) Gill: *Tsuga heterophylla* (Rafinesque) Sargent*, *T. mertensiana* (Bongard) Sargent*:

A. campylopodum forma *typicum* Gill: *Pinus attenuata* Lemmon, *P. contorta* Loudon, *P. coulteri* D. Don, *P. jeffreyi* "Oreg. Com."*, *P. ponderosa* Lawson, *P. radiata* D. Don, *P. sabiniana* Douglas.

Arceuthobium douglasii Engelm.: *Pseudotsuga taxifolia* (Lamarck) Britton.*

While the disease is now known only on the above hosts in the localities indicated in Text fig. 1, it seems logical to suspect that its distribution may be limited only by the range of those species on which it is now known, and additional surveys and inoculation studies may show that the fungus is capable of attacking other species of *Arceuthobium*.

THE CAUSAL FUNGUS

Description and Classification

Microscopic examination showed that the causal fungus belonged to the Fungi Imperfecti. While asexual conidia are produced in great abundance, accumulating in white masses that are one of the most striking features of the disease, no perfect stage has as yet been found. Whereas early observations indicated that it did not conform to any known species, but in some respects resembled *Fusarium* (Ellis, 1939), subsequent work has shown that it more properly belongs in the form genus *Septogloeum*. A review of the literature and comparisons with herbarium material failed to reveal any identical or closely related species. Inasmuch as no similar fungus is known on *Arceuthobium* and the organism does not conform to any described member of the genus *Septogloeum*, it is regarded as a new species which is described as follows:

Septogloeum Gillii sp. nov.

Fruiting bodies subcuticular, subepidermal or rarely below 1 or 2 layers of cortical parenchyma, covered or erumpent, scattered, irregularly circular to oblong in outline, 0.16–2.0 mm. in diameter, or confluent into continuous layers 2–8 mm., occasionally up to 14 mm. long, frequently girdling the stem; basal stromatic layer compact, hyaline, 10–19 μ thick; conidia hyaline, granular, cylindrical to fusiform, straight or slightly curved, continuous, (6.2) 12–15 (25.7) x (2.6) 3.2–3.4 (5.1) μ, or 1-septate (6.8) 16–24 (34.2) x (2.6) 3.3–3.7 (5.1) μ, occasionally 2-septate 22–38 x 3.4–4.8 μ, or 3-septate 27–41 x 3.4–5.1 μ, borne singly but repetitiously at the tips of the conidiophores, accumulating in white slimy masses, chalky and hard when dry; conidiophores simple or branched, continuous or septate, hyaline, 10–51 x 1.4–2.2 μ.

Parasitic on shoots of *Arceuthobium campylopodum* and *A. douglasii* in Western United States.

Fructificationes subcuticulares, subepidermicales vel rare sub stratis 1–2 corticalibus sitae, tectae vel erumpentes, conspersae, irregulariter circulares usque oblongae, 0.16–2.0 mm. diam. vel in stratis 2–8 mm., rare usque 14 mm. longis confluentes, caulem saepe cingentes; stratum basale compactum, hyalinum, 10–90 μ crassum; conidia hyalina, granulosa, cylindrica usque fusiformia, recta vel curvula, continua usque 1–3-septata, 6.2–41 x 2.6–5.1 μ, ex apicibus conidiophororum singulatim sed repetite oriunda, in massas albas glutinosas, siccas cretaceas durasque, accumulata; conidiophora simplicia vel ramosa, continua vel septata, hyalina, 10–51 x 1.4–2.2 μ.

In surculis *Arceuthobii campylopodi* et *A. douglasii* in regione occidentali, U. S. A.

The following specimens in the herbarium of the Division of Forest Pathology at Albuquerque, New Mexico, were examined: (Instances in which the disease was found on herbarium collections of the host are indicated by an asterick (*)).

On *Arceuthobium campylopodum* f. *abietinum* (Engelmann) Gill

Arizona. Coconino County; Grand Canyon, Gill, August 26, 1934 (68297); Gill and Ellis, June 2, 1939 (89417).

California. Calaveras County; Dorrington, Wright, May 25, 1932 (68123)*.
Oregon. Josephine County; Oregon Caves, Root and Gooding, August 1, 1932 (68274)*.
Washington. Pierce County; Longmire, Gill, August 20, 1932 (68197).

On *A. campylopodum* f. *blumeri* (A. Nelson) Gill

Arizona. Graham County; Graham Mountains, Stauffer and Gill, July 22, 1934 (68293)*. Pima County; Santa Catalina Mountains, Gill, June 3, 1932 (68130)*.

On *A. campylopodum* f. *cyanocarpum* (A. Nelson) Gill

Arizona. Cochise County; Chiricahua Mountains, Gill and Ellis, March 22, 1939 (89404); Ellis, June 23, 1939 (89423); Gill and Ellis, January 14, 1940. (89432); Mielke and Ellis, September 10, 1944 (89695). Graham County; Graham Mountains, Gill, September 25, 1936 (89313); Ellis, November 23, 1938 (89401), May 23, 1939 (89415), June 22, 1939 (89421), August 21, 1939 (89429); Mielke and Ellis, September 11, 1944 (89693). Greenlee County; Blue Summit, Ellis, May 21, 1939 (89413). Pima County; Santa Catalina Mountains, Gill and Ellis, March 25, 1939 (89407), Ellis, June 24, 1939 (89424); Mielke and Ellis, September 7, 1944 (89696).
Utah. Garfield County; Bryce Canyon, Gill, June 25, 1932 (68144)*.

On *A. campylopodum* f. *divaricatum* (Engelmann) Gill

Arizona. Coconino County; Grand Canyon, Gill, June 6, 1932 (68234)*; Jacob's Lake, Gill and Ellis, June 3, 1939 (89419); Mielke, September 30, 1944 (89700). Long Valley, Ellis, July 2, 1939 (89426).
California. San Bernardino County; Bear Lake, Gill and Wright, September 25, 1931 (68064)*.
New Mexico. Bernalillo County; Sandia Mountains, Ellis, April 22, 1939 (89411).

On *A. campylopodum* f. *microcarpum* (Engelmann) Gill

Arizona. Coconino County; Grand Canyon, Gill and Ellis, June 2, 1939 (89418). Graham County; Graham Mountains, Gill, July 17, 1934 (68290), Gill and Stouffer, July 21, 1934 (68310), Ellis, November 23, 1938 (89402), May 22, 1939 (89414), June 22, 1939 (89422), August 21, 1939 (89428), Mielke and Ellis, September 12, 1944 (89692) *TYPE*. Greenlee County; Blue Summit, Gill, July 3, 1934 (68305)*, Ellis, May 21, 1939 (89412).

On *A. campylopodum* f. *tsugensis* (Rosendahl) Gill

California. Siskiyou County; Kidder Creek, Gill, August 3, 1932 (68180)*.
Washington. Pierce County; Mt. Rainier National Park—White River entrance, Gill, August 19, 1932 (68196)*; Longmire, Gill, August 20, 1932 (68199).

On *A. campylopodum* f. *typicum* Gill

Oregon. Joesphine County; Wonder, Mitchell, July 23, 1932 (68212)*.

On *Arceuthobium douglasii* Engelm

Arizona. Graham County; Graham Mountains, Ellis, August 21, 1939 (89427); Mielke and Ellis, September 13, 1944 (89698). Pima County; Santa Catalina Mountains, Gill and Ellis, March 25, 1939 (89406), Ellis, June 24, 1939 (89425).

New Mexico. Bernalillo County; Sandia Mountains, Gill and Long, June 13, 1932 (68136)*.

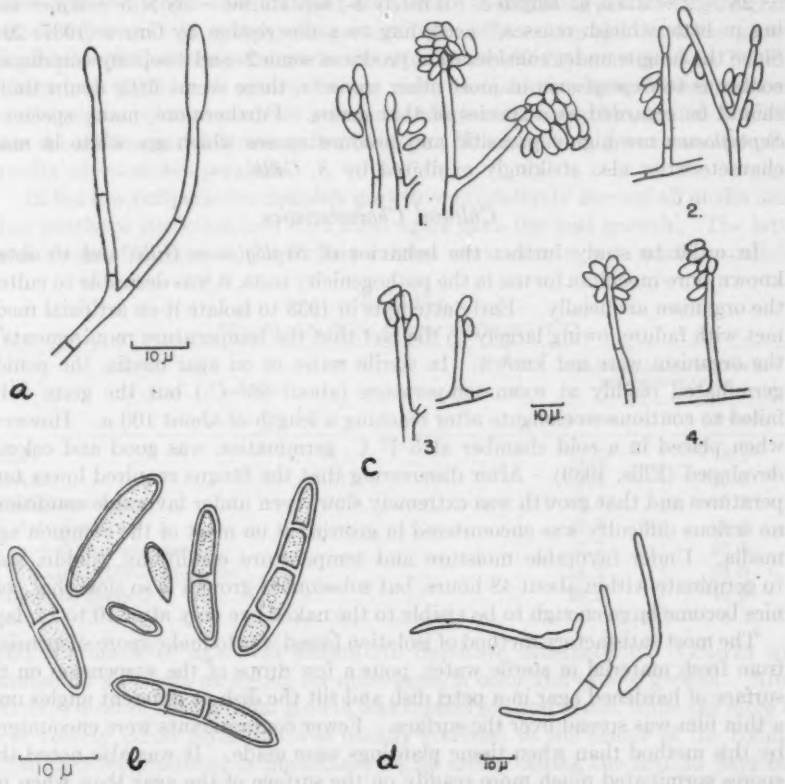
In addition to the collections on file at Albuquerque and the University of North Carolina, portions of the type collection are being deposited with the Mycological Collections of the Bureau of Plant Industry, Soils and Agricultural Engineering and in the Farlow Herbarium of Harvard University.

Because of variations in spore size and septation and the characteristics of the fruiting structure, it was somewhat difficult to determine the proper taxonomic position of the fungus. It was at first tentatively referred to the genus *Fusarium*, largely on the basis of spore form and because in culture it produced relatively small one-celled spores, borne singly but adhering in loose heads at the tips of the hyphae, which resembled the microconidial stages of certain species of that genus. However, further study showed that the conidia produced in nature were not typical of the Fusaria and the sub-cuticular or sub-epidermal development of the fungus indicated that it belonged in the Melanconiales. There was at first some question in the writer's mind on the latter point, owing to the fact that often the fungus appeared to form no clear-cut acervuli but instead fruited in extensive, continuous layers, often completely girdling the stem and extending along it longitudinally for several millimeters (Pl. 4, fig. 2a and c). However, subsequent microscopic studies on the early stages of the disease showed that the fruiting primordia originated in numerous small acervulus-like bodies along the stem, which later became confluent (Pl. 5, fig. 1 a-d).

Determination of the generic affinity of the fungus was also a difficult problem. Sections and mounts from separate diseased plants in the same collection, or even from separate lesions on one plant, showed conidia which differed markedly in size and septation (Text fig. 2 b, and Pl. 5, fig. 2). In some instances only non-septate conidia were observed; in others they were predominately one-septate, while often 0-, 1-, 2-, and 3-septate conidia were present in the same fruiting body. In fruiting bodies still covered by the epidermal layer, the conidia were usually non-septate, while erumpent stages often contained an abundance of septate ones. Thus, on the basis of septation, the genera *Gloeosporium*, *Septomyxa*, and *Septogloeum* were indicated by separate fruits and collections. However, germination tests and culture studies showed that the conidia were all produced by the same fungus. Both non-septate and septate conidia of all sizes germinated quite readily and single-spore isolations of both gave rise to the same type of growth in culture. On germination, septate conidia usually produced two germ tubes, one from the tip of each outer cell, but somtimes only one cell germinated. Single-celled spores, on the other hand, produced either one or two germ tubes. While 0- or 1-septate conidia were most frequently observed,

the fact that occasionally 2- and 3- septate ones occurred seemed to be sufficient reason for excluding *Gloeosporium* and *Septomyxa*.

The use of spore septation as a character for separating various genera in the Fungi Imperfecti has lead to a great deal of confusion. For example, many



TEXT FIG. 2, a and b, *Septogloeum Gillii* from host: a, portion of branched conidiophore; b, conidia. c and d, *S. Gillii* from culture: c, spore production in strains 1–4; d, germinating conidia.

species have been described in the genus *Gloeosporium*, which have later been transferred to *Marssonina* or *Septogloeum* because of the discovery later of septate spores. Species of the latter as well as other genera are often described as having spores "—septate at maturity," "—finally—septate," or "—ultimately—septate." The criteria for determining maturity of such conidia are poorly defined. The ability of spores to germinate and produce new growth surely indicates maturity in one sense, yet in many species both continuous and septate ones germinate readily.

According to the generic description of *Septogloeum* (Saccardo, Sylloge 3:

801. 1884), the conidia are 2- to many-septate. However, numerous species have been described with continuous to many-septate ones. For example, *S. equiseti* Tehon has continuous to 4-septate spores (Tehon, 1937), and, in *S. ulmi* Died., the spores are "—continuous, guttulate or granular, after a time 1-septate, 20 − 28 × 2 − 3.5 μ, at length 3- (or rarely 4-) septate, 30 − 58 × 5 − 6 μ, —issuing in little whitish masses," according to a description by Grove (1937: 291). Since the fungus under consideration produces some 2- and 3-septate conidia and conforms to *Septogloeum* in most other respects, there seems little doubt that it should be regarded as a species of that genus. Furthermore, many species of *Septogloeum* are highly parasitic and produce spores which are white in mass, characteristics also strikingly exhibited by *S. Gillii*.

Cultural Characteristics

In order to study further the behavior of *Septogloeum Gillii* and to obtain known pure inoculum for use in the pathogenicity tests, it was desirable to culture the organism artificially. Early attempts in 1938 to isolate it on artificial media met with failure, owing largely to the fact that the temperature requirements of the organism were not known. In sterile water or on agar media, the conidia germinated readily at room temperature (about 25° C.) but the germ tubes failed to continue to elongate after reaching a length of about 100 μ. However, when placed in a cold chamber at 5–7° C. germination was good and colonies developed (Ellis, 1939). After discovering that the fungus required lower temperatures and that growth was extremely slow, even under favorable conditions, no serious difficulty was encountered in growing it on most of the common agar media. Under favorable moisture and temperature conditions, conidia start to germinate within about 48 hours, but subsequent growth is so slow that colonies become large enough to be visible to the naked eye only after 10 to 14 days.

The most satisfactory method of isolation found was to make spore suspensions from fresh material in sterile water, pour a few drops of the suspension on the surface of hardened agar in a petri dish and tilt the dish at different angles until a thin film was spread over the surface. Fewer contaminants were encountered by this method than when tissue plantings were made. It was also noted that spores germinated much more readily on the surface of the agar than when immersed in it by the ordinary dilution-plate technique. All single spore isolations were made by the method described by Lambert (1939), in which a "biscuit cutter," slightly smaller in diameter than the microscope field under low power, is mounted on the microscope and used to cut out a column of agar on which the spore has been located.

On March 12, 1939, a test was initiated in which growth of the fungus was compared on 7 agar media in a temperature chamber held at 5–7° C. A duplicate series was run at room temperature which fluctuated between about 22° and 28° C. An isolate from *A. campylopodum* f. *cyanocarpum* was used in the test. The agars were poured to even depths in 90 mm. petri dishes and the plates seeded with transfer disks, approximately 4 mm. in diameter, cut with a sterile cork borer from the margin of a colony on malt agar. Two plates of

each medium were employed at each of the two temperatures and growth was measured at intervals of 15 days. The media were either Difco brand or were prepared according to standard laboratory formulae. The mistletoe decoction agar was prepared by steeping 20 grams of dried mistletoe shoots in 1000 ml. of distilled water for 30 minutes at about 95° C., decanting and adding 20 grams of dextrose and 18 grams of agar-agar per liter. Average diameter growth figures for the low temperature series, after 30 and 60 days, are given in Table 1. There was little or no growth in the room temperature series where, on bean dextrose, the colonies made an average total growth of only 5 mm. and on mistletoe decoction agar of 3 mm., after 60 days. There was no growth on the other media at room temperature.

In the low temperature chamber growth was relatively slow on all media used, but mistletoe decoction and corn meal agars gave the best growth. The latter was chosen for most of the further culture work since it was readily available

TABLE 1

Growth of S. Gillii on agar media at 5–7°C.

MEDIUM	AVERAGE DIAMETER GROWTH IN MILLIMETERS AFTER	
	30 days	60 days
Malt	11.5	18.5
Bean	5.5	22.0
Bean-Dextrose	13.0	29.0
Potato-Dextrose	13.5	28.5
Prune (Difco prepared)	5.5	20.5
Corn meal (Difco prepared)	14.0	33.0
Mistletoe decoction	20.5	40.0

and the mistletoe agar was difficult to duplicate satisfactorily. Growth was similar on all media excepting for differences in color and rate of growth. After 60 days most of the mycelial growth was submerged and dense, while the more or less velvety aerial mycelium was usually confined to the center of the colony. Conidia were produced in abundance on all media during the first 30 days but less profusely thereafter.

The fungus has been isolated from 5 different host sources and has been differentiated into 4 strains on the basis of cultural characteristics and hosts, as shown in Table 2. These observations were made on cultures used in the temperature relations experiments, in which, as will be shown later, it was found that all strains had essentially the same temperature requirements. More detailed descriptions of the 4 strains are given below. The color designations used in describing cultures are based on Ridgway (1912).

Strain 1. At first white, dense fine velvety surface and dense submerged mycelium. Subsequent radial growth mostly submerged; center $\frac{1}{4}$ to $\frac{1}{2}$ of colony with compact velvety aerial hyphae; passing through deepening shades of salmon color to Sanford's brown center and maize yellow margin after 30–45 days; margin regular.

Strain 2. Same as strain 1 except for pigmentation; at first white, later with pale salmon color center and light mineral gray margin or light mineral gray throughout.

Strain 3. At first like strain 1; later with light mineral gray margin and dense velvety white center.

Strain 4. At first like strain 1; later with a narrow margin of light mineral gray and center ½ to ⅔ of colony with white compact woolly surface after 30–45 days; occasionally forming a rather hard, tough, stroma-like mat on surface of agar, covered with fine velvety hyphae throughout.

TABLE 2

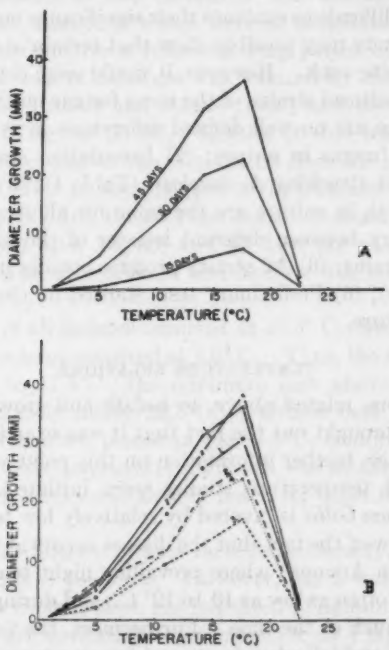
Characteristics of 4 cultural strains of S. Gillii after 30 days growth on Difco Brand corn meal agar at 17.5°C.

STRAIN NO.	HOST	AVE. COLONY DIAMETER	COLOR	TYPE OF GROWTH
		mm.		
1	*A. campylopodum f. cyanocarpum*	21.8	Margin maize yellow; center Sanford's brown	Mostly submerged; center compact, velvety
1	do.	18.9	do.	do.
1	*A. campylopodum f. microcarpum*	25.0	do.	do.
2	*A. campylopodum f. abietinum*	17.6	Margin light mineral gray; center pale salmon color	do.
3	*A. campylopodum f. divaricatum*	12.4	Margin light mineral gray; center white	do. Radiating white lines to margin
4	*A. douglasii*	15.9	Margin light mineral gray; center white	Less submerged and more aerial hyphae; surface compact woolly

These characteristics have remained quite constant through repeated transfers as well as in reisolations following inoculations. For example, strain 1, when used as inoculum on *A. douglasii* and reisolated, retains its characteristic color. Repeated single spore isolations from the same hosts in general show the same characteristics. The pale salmon color of strain 2, suggestive of the same pigment found in strain 1, is not always discernible. The pigment characteristic of strain 1 is always present on all media, but varies in intensity. Isolates of strain 4 vary in growth habit but usually produce more aerial mycelium and they often form a hard stroma-like mat on the surface of the agar. In preliminary tests, when all 4 strains were grown together in the same plate they retained their individual characteristics but showed no clear-cut evidence of incompatibility, which suggests that they are at least very closely related. As indicated in Table 2, isolates of strain 1 usually make the most growth and those of strain 3

the least. However, there was also considerable variation in growth rates of the different isolates of strain 1.

Spore production in all strains is abundant but, as noted above, decreases with the age of the culture. After several transfers on corn meal agar, some isolates of strain 4 have ceased to sporulate, but, when transferred to media containing asparagin, sporulation was resumed. Conidia are produced successively at the hyphal tips and usually adhere in loose heads (Text fig. 2c). They are usually continuous when produced, septate spores appearing in quantity only after



TEXT FIG. 3. Growth of *Septogloeum Gillii* on corn meal agar at controlled temperatures: A, strain 1 after 15, 30, and 45 days; B, three isolates of strain 1 and one isolate each of 2, 3, and 4 after 45 days.

cultures are several days old. Spore size and septation is extremely variable, even between different isolates of the same strain. For example, 60-day old cultures of one isolate of strain 1 may contain about 50 per cent non-septate, and 50 per cent 1-septate, conidia, 5–19 μ long, while another isolate, from the same host, may produce almost exclusively non-septate conidia, 5–14 μ long, when grown simultaneously under identical conditions. Continuous conidia are found in artificial culture more frequently than septate ones and more than 1-septate conidia are encountered only rarely. Both septate and non-septate conidia germinate readily (Text fig. 2d), a point also noted above for those

produced in nature. Strain 1 usually produces somewhat larger and more frequently septate conidia, more typical of those found in nature, than the other strains.

All strains grow well on autoclaved rice and spore production is profuse on rice plugs to which asparagin has been added. In strains 1 and 2 the spores often accumulate on this medium in white chalky masses, which resemble the spore masses found in nature. Such masses have not been observed in strains 3 and 4 on the rice-asparagin medium, but spores are produced abundantly.

While several rather marked cultural differences are thus apparent between these 4 strains, it is difficult to evaluate their significance on the basis of the work to date. Further study may possibly show that certain of them should be given varietal or even specific rank. However, it would seem desirable for the present to classify them as cultural strains of the same fungus on the basis of the following points: (1) There are no well defined differences in symptoms produced or morphology of the fungus in nature; (2) Inoculation studies show that all 4 strains are capable of attacking *A. douglasii* (Table 4); (3) The temperature requirements for growth in culture are the same for all strains (Text fig. 3); (4) Rates of growth vary between different isolates of the same strain as well as between different strains; (6) All strains produce conidia in the same manner in culture (Text fig. 2c); (6) Preliminary tests showed no clear-cut evidence of incompatibility in culture.

TEMPERATURE RELATIONS

The early attempts, related above, to isolate and grow the causal organism in culture, forcibly brought out the fact that it was exacting in its temperature requirements. Hence, further information on this point was particularly desirable and controlled temperature studies were initiated. As already noted, growth of *Septogloeum Gillii* is favored by relatively low temperatures. This is not surprising in view of the fact that the disease occurs at rather high elevations (6500 to 9500 feet in Arizona) where prevailing night temperatures during the summer months are often as low as 10 to 12° C., and during the winter are below the freezing point much of the time. Furthermore, the fungus is active during periods in the spring and fall when frosts and freezing temperatures often prevail.

The generally accepted procedure for measuring the effect of temperature on fungous growth is to determine the increase in diameter of colonies in agar plate cultures held at constant temperatures. The results of such workers as Fawcett and Barger (1927), Tisdale (1917), and Lindgren (1933) show that this method is satisfactory and that there is substantial agreement between optimum temperatures for colony growth and intensity of effects on natural hosts.

The fungus was grown on Difco Brand corn meal agar poured as nearly as possible to even depths in 90 mm. petri dishes. Six isolates were tested simultaneously, two from *A. campylopodum* f. *cyanocarpum* (strain 1), and one each from *A. campylopodum* f. *microcarpum* (strain 1), *A. campylopodum* f. *abietinum* (strain 2), *A. campylopodum* f. *divaricatum* (strain 3), and *A. douglasii* (strain 4). Disks approximately 2 mm. in diameter were cut from the margins of 30-day

old petri dish colonies of single spore cultures on corn meal agar, by means of a sharpened cork borer and transferred with a sterile needle to the center of each plate. Five replicate plates of each culture were placed in each of 6 temperature chambers ranging from 1.0° to 22.5° C. Temperature fluctuations were usually only 1.5° C. or less. Maximum fluctuations of up to 3° C. were occasionally noted, but they were always of short duration and are not believed to have altered seriously the results. Due to the relatively slow growth of the fungus, measurements were made only at 15, 30, and 45-day intervals. Colony diameters were measured in two directions and averaged. The tests were run in duplicate series, results of which were in substantial agreement. Since each experiment extended over a relatively long period of time, a third series was run in which the loss of moisture was reduced by the use of wide rubber bands as described by Hubert and Harris (1930) and previously used in temperature studies by Wagener (1939). Results of this test showed that there was no appreciable effect due to loss of moisture from the plates.

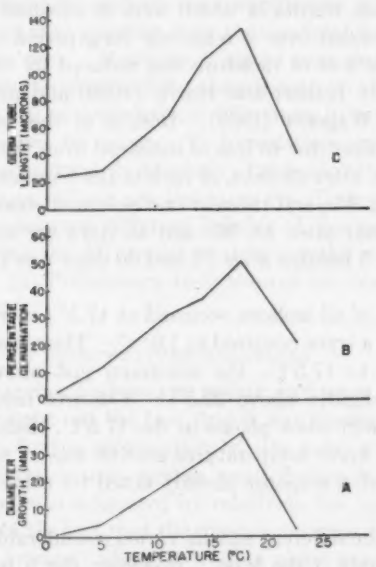
Average diameters, after 45 days, of each of the 6 isolates at each temperature are shown in Text fig. 3B, and those of one isolate of strain 1 (from *A. campylopodum* f. *cyanocarpum*) after 15, 30, and 45 days are shown in Text fig. 3A. Growth of the other 5 isolates after 15 and 30 days was proportional to that at 45 days.

Maximum growth of all isolates occurred at 17.5° C., while growth was slight at 22.5° C., and only a trace occurred at 1.0° C. Thus, the indicated optimum is probably very close to 17.5°C., the minimum just above the freezing point, and the maximum slightly above 22.5°C. Cultures held at 1.0° and 22.5°C. resumed normal growth when placed in the 17.5°C. chamber at the conclusion of the test. At the lower temperatures growth was at first slow but increased as the test progressed, a response already noted for other fungi (Fawcett, 1921; Lindgren, 1933).

Growth rates for the different strains varied considerably, strain 1 making the most growth and strain 3 the least. However, the 3 isolates of strain 1 also varied in rate of growth and, since the indicated minimum, maximum, and optimum temperatures are in essential agreement for all 4 strains, the differences are probably no greater than might be expected for different strains of the same organism.

Studies were also made on the effect of temperature on spore germination. Spore suspensions were made from a single spore culture, isolated from *A. campylopodum* f. *cyanocarpum* growing on steamed rice, and spread evenly over the surface of corn meal agar in petri dishes. These were incubated at the same temperatures employed in the above tests and the germination percentages and germ tube lengths determined at 24-hour intervals. After the first 24 hours no growth was observed at any temperature. After 48 hours a few spores were starting to germinate at all but the lowest 2 temperatures, while germination occurred at all 6 temperatures after 72 hours. Results of these counts and measurements on the 6th day (144 hours) are shown in Text fig. 4, which also shows, for purposes of comparison, the average diameter growths of the same

isolate after 45 days (Text fig. 4A). The germination percentages indicated (Text fig. 4B) are each based on counts of 100 spores and the germ tube lengths (Text fig. 4C) are averages of 10 measurements at each temperature. Results are essentially in agreement with those for colony growth, excepting that more germination and growth of germ tubes occurred at 22.5° C. than at 5° C. This can probably be ascribed to the slow initial response at the lower temperatures already noted above. It is noteworthy that 17.5° C. was the most favorable temperature for spore germination, germ tube elongation, and growth in culture.



TEXT FIG. 4. Effect of temperature on (A) colony growth after 45 days; (B) germination of conidia after 6 days; and (C) elongation of germ tubes after 6 days. Graphs for a single isolate of *Septogloeum Gillii*.

Dissemination

Most fungi are disseminated by spores which may be carried by wind, rain, insects, birds, and other animals (Boyce, 1938: 24; Smith, et al., 1933). Observations indicate that *Septogloeum Gillii* may be disseminated in several ways. As pointed out above, spores are produced in abundance, and adhere to each other in large, white masses clearly visible to the naked eye. The organism appears to be largely dependent on its host for moisture, as evidenced by the fact that active fruiting occurs in lesions on still living shoots, even during dry weather. After the host is killed, however, the spore masses become dry and hard. Dissemination by wind alone is thus improbable, but the conidia are undoubtedly spread locally by the splattering and blowing of rain water. Thin,

white deposits of conidia have often been observed on the bark of twigs and branches bearing heavily infected mistletoe shoots. These deposits are most noticeable following periods of rainy weather.

Arceuthobium is spread locally by the violent expulsion of the seed from the berry. According to Dowding (1929) the seed may be shot as far as 33 feet horizontally. While fruit infection by *S. Gillii* is not particularly common, it has often been observed in nature as well as produced by inoculation, and it seems possible that the disease might be carried along with the seed from infected fruits.

The long distance spread of *Arceuthobium* is accomplished largely by birds and other animals (Gill, 1935) and it seems probable that they may also help to spread anthracnose.

Insects may play a rather important rôle in dissemination. The dwarf mistletoes are largely dependent on insects for pollination. Weir (1915) stated that hymenopterous insects were most important but that other orders seemed to be involved. Tubeuf (1919) thought that the absence of the proper insects was responsible for his failure to obtain mature fruits of *Arceuthobium* in greenhouse experiments. Stigmatic exudations have been noted by Dowding (1931) on *A. americanum* and by Heinricher (1915) on *A. oxycedri*. The writer has noted such exudations on most species in the Southwest, particularly on *A. douglasii*, and that insects, especially flies and ants, appear to be attracted by them in great numbers. Insects, especially ants, were also observed in non-flowering pistillate clusters as well as among groups of staminate shoots. Dowding (1931) has suggested that ants play a rôle in the dissemination of *Wallrothiella*. As mentioned previously, spittle insects often attack mistletoe shoots and these have at times been observed attacking plants affected with anthracnose.

The above observations strongly indicate that *S. Gillii* is spread locally largely by means of insects, rain, or a combination of rain and wind, and that birds and other animals may carry it over longer distances.

INOCULATION STUDIES

A series of inoculation experiments was undertaken to determine whether or not the associated fungus was indeed the causal organism and to obtain as much information as possible on the mode of infection, incubation period, and host range of the parasite. Since *Septogloeum Gillii* was the only constantly associated organism and had been repeatedly isolated at all stages in the development of the disease, there was reason to believe that it was the pathogen and the only organism involved, but positive proof was lacking. Variation in spore types as well as cultural characteristics of isolates suggested the possibility of different strains of the fungus and it was also hoped that cross inoculation results might throw some light on this problem.

Because the mistletoe host of the fungus is also a parasite dependent in turn upon its tree host, it was difficult to carry out inoculation studies under controlled conditions. Several attempts were made to inoculate mistletoe on small twigs kept alive for a few weeks in cool temperature chambers in the laboratory,

but while in a few cases inoculated shoots died somewhat earlier than uninoculated controls, no true symptoms of the disease were produced. Several species of small trees infected with mistletoe were transplanted to a lath house constructed in Albuquerque and the mistletoe inoculated with the fungus. In this test, infection resulted on only a relatively low percentage of shoots inoculated, due primarily, it is believed, to environmental conditions unfavorable to the normal development of the trees and mistletoes, as well as the fungus.

Under field conditions the great majority of inoculation trials were successful, but such tests were necessarily somewhat limited in scope due to the relative inaccessibility of the host. *Arceuthobium douglasii*, which occurs in the Sandia Mountains within about 30 miles (by auto) of Albuquerque was the most accessible, and as a result was the host most frequently employed for inoculation purposes. In most instances the tests were conducted in areas where the disease was unknown, or at reasonably safe distances from known infections. Uninoculated controls were employed in sufficient numbers to detect any occurrence of natural infection.

All inoculum was taken from pure, usually single spore, cultures on agar or rice media and consisted either of spore suspensions in sterile water, or of mycelium and spores in or on the media. Spore suspensions were applied with a sterile camel hair brush and cultures were applied with sterile scalpels, needles or other suitable instruments. Inoculum was applied either directly to uninjured shoots or to wounded shoots. Wounds consisted either of tiny slits made with a ½ arrow point needle, into which bits of inoculum were inserted, or, of tiny needle puncture wounds, over which spore suspensions were painted. In a few early attempts the shoots were covered with small bits of moistened sterile cotton after inoculation, but this proved to be of doubtful value and was abandoned. All control shoots were treated in exactly the same manner as inoculated ones excepting that sterile water and media were substituted for spore suspensions and cultures of the fungus. Results were considered positive only when inoculated shoots showed clear-cut disease symptoms. In most instances the fungus had at least started to fruit by the time final results were recorded. In order to facilitate reisolation and to guard against loss of dead shoots, inoculated plants were usually collected and results recorded before death occurred. Reisolations were made in a sufficient number of tests to demonstrate conclusively that the fungus could be recovered. The reisolates were identical morphologically and culturally with the original cultures and when used again as inoculum produced symptoms typical of the disease.

The results of all field and lath house inoculations are given in Table 3. Plate 6, fig. 2 shows the symptoms of the disease on *A. douglasii* produced by artificial inoculation. It is clearly evident from these results that *Septogloeum Gillii* is indeed the causal organism and is an extremely virulent parasite, and, since most inoculations were carried out in the open with no special effort to protect the inoculum from drying, it would appear that infection may be established with comparative ease.

The large number of positive results obtained without wounds of any kind,

by merely applying spore suspensions or mycelium and spores on agar, shows that the fungus is not a wound parasite and indicates that direct penetration occurs. This may be questioned in the case of *A. campylopodum* f. *divaricatum* on which most of the positive results were from wound inoculations. However, the site where inoculations on this host were conducted was relatively dry and open, conditions not generally favorable for initiation of infection. Furthermore, there is no evidence that wound infection is necessary where the disease occurs naturally on this host.

On *A. campylopodum* f. *cyanocarpum* only one of 43 inoculated shoots became infected, but it showed clear-cut symptoms of the disease. This was a lath house test and the host, growing on *Pinus flexilis*, came from a location near Kingston Pass, in Sierra County, New Mexico, where the mistletoe is not abundant and the fungus has never been observed. As previously noted, however, this host is severely affected in other areas.

Only wound inoculations were successful on the ponderosa pine mistletoe (*A. vaginatum* f. *cryptopodum*), on which the disease does not occur in nature. On this host the disease was manifest only by necrotic areas spreading from the point of inoculation (Pl. 6, fig. 1). No symptoms typical of the disease on other hosts were observed. However, shoots were sometimes completely girdled and killed and the fungus was easily recovered in culture.

Most inoculations initiated in the spring or early summer were successful, while those put in during the fall and winter usually resulted in failure. This probably indicates that natural infection occurs in the spring and summer, although it could possibly have been merely the result of unfavorable environmental conditions prevailing at the particular time the fall and winter inoculations were made.

The differences in susceptibility of staminate and pistillate plants, noted under natural conditions, were not clearly indicated in the inoculation results. The tests were not set up with this point in view, however, and few direct comparisons are possible. Nevertheless, staminate plants were successfully inoculated in a number of instances.

Due to travel distances involved, it was not possible to make frequent visits to inoculation plots. However, observations indicated that the incubation period was about 60 days. Tiny visible lesions were noted as early as 54 days after inoculation, but usually only after 60 days or more.

The results of cross inoculation attempts are summarized in Table 4. Isolates were available only from 4 forms of *A. campylopodum* and from *A. douglasii* and only 3 forms of the former and the Douglas fir mistletoe were accessible for inoculation purposes. All isolates produced typical symptoms on *A. douglasii*, and positive results were obtained in all other instances when cross inoculations were attempted. In addition, isolates from *A. campylopodum* f. *cyanocarpum* were pathogenic on *A. vaginatum*. These results lend support to the contention that the cultural strains previously described are variations of the same fungus.

EFFECT OF THE PARASITE ON THE HOST

Macroscopically the effect of the parasite on the host is evidenced in the production of numerous lesions on all parts of the stem and occasionally on the

TABLE 3

Results of inoculations with Septogloeum Gillii

HOST INOCULATED		DATE	LOCATION[1]	INOCULUM		WOUNDS[4]	NUMBER OF SHOOTS			
							Inoculations		Controls	
Name	Sex			Source[2]	Type[3]		Total[5]	Percent Positive	Total	Percent Positive
A. campylopodum f. *cyanocarpum*	♀	5-15-40	A.	b	ss	n	43	2	51	0
A. campylopodum f. *divaricatum*	do.	4-10-39	M.	a	ac	s	10	40	10	0
	do.	do.	M.	a	ss	np	5	40	4	0
	do.	do.	M.	a	ss	n	5	0	4	0
	♂	9-27-39	M.	a	ss	n	10	0	10	0
	♀	4-4-40	M.	d	ac	s	19	42	8	0
	♂	do.	M.	d	ac	n	10	10	10	0
A. campylopodum f. *microcarpum*	do.	5-22-39	G.	a	ss	n	12	50	23	0
	♀	do.	G.	a	ac	n	15	67	10	0
	do.	5-9-40	G.	b	ac	n	28	68	30	10
	do.	5-15-40	A.	b	ss	n	17	30	12	0
A. douglasii	do.	4-23-39	S.	a	ss	n	58	62	114	0
	do.	do.	S.	a	ss	n	196	33	267	0
	♂	9-27-39	S.	a	rc	n	(14)	7	(4)	0
	♀	do.	S.	a	rc	n	(14)	0	(4)	0
	do.	12-1-39	S.	e	ac	n	(4)	0	(2)	0
	♂	4-5-40	S.	b	ac	n	228	17	22	0
	do.	do.	S.	e	ac	n	37	24	25	0
	♀♂	do.	S.	e	ac	n	219	28	19	0
	♀	4-24-40	A.	b	ss	n	8	25	8	0
	♂	do.	A.	b	ss	n	10	40	8	0
	♀	4-30-40	A.	e	ss	n	27	4	10	0
	do.	do.	A.	e	ac	n	11	0	15	0
	do.	do.	A.	a	ac	n	7	14	10	0
	do.	do.	A.	a	ss	n	46	0	10	0
A. vaginatum f. *cryptopodum*	do.	4-10-39	M.	a	ss	np	10	10	10	0
	do.	do.	M.	a	ss	n	5	0	5	0
	do.	do.	M.	a	ac	s	12	67	6	0
	do.	2-6-40	M.	a	ac	s	15	53	10	0
	do.	4-4-40	M.	a	ac	s	10	90	5	0

[1] A—lath house, Albuquerque; M—Manzano Mountains, New Mexico; G—Graham Mountains, Arizona; S—Sandia Mountains, New Mexico.

[2] a—*A. campylopodum* f. *cyanocarpum* (strain 1). b—*A. campylopodum* f. *microcarpum* (strain 1). c—*A. campylopodum* f. *abietinum* (strain 2). d—*A. campylopodum* f. *divaricatum* (strain 3). e—*A. douglasii* (strain 4).

[3] ss—spore suspension; ac—agar culture; rc—rice culture.

[4] n—no wounds; s—slit wounds; np—needle puncture wounds.

[5] Figures not in parentheses refer to numbers of individual shoots; figures in parentheses ( ) refer to numbers of clusters, each consisting of from 5 to 30 shoots.

fruits. The fruiting bodies are at first covered by the cuticularized epidermal layer but later erupt through this protective covering, exposing the fungus and the internal tissues of the host. The ultimate effect on the mistletoe plant is death, but observations indicate that this is a relatively slow process. Usually during the early covered stages the hosts show some evidence of stunting and the berries are often somewhat withered and smaller than on healthy shoots. Death may occur at this stage but more commonly the shoots remain alive until after the fungus has ruptured the epidermal covering. Even after this occurs the plants often remain alive for a considerable length of time. Still living shoots often have the major portion of the stems involved in continuous, large, open lesions (Pl. 4, fig. 2a and c). This rather slow advent of death of the shoots may be a factor which favors the development of the fruiting bodies of the fungus into such relatively large, continuous layers.

Preliminary microscopic observations showed that the tissues of the cortex and stele were filled with a profuse intercellular mycelium (Gill, 1935; Ellis, 1939).

TABLE 4

Summary of cross inoculation results

SOURCE OF INOCULUM	HOSTS SUCCESSFULLY INOCULATED			
	A. campylopodum			*A. douglasii*
	f. *cyanocarpum*	f. *microcarpum*	f. *divaricatum*	
A. campylopodum f. *cyanocarpum*		+	+	+
A. campylopodum f. *microcarpum*	+	+		+
A. campylopodum f. *abietinum*				+
A. campylopodum f. *divaricatum*			+	+
A. douglasii				+

Further studies on free hand and microtome sections of diseased host tissue have been made. The free hand sections were usually made from fresh material and mounted in water, glycerine, or solutions of cotton blue, picro-analine-blue, or lacto-phenol. For microtome sectioning fresh material was killed either in alcohol-formalin-acetic acid or glycerine-alcohol solutions, embedded in paraffin by the butyl alcohol method, sectioned, and stained with iron-alum-haematoxylin. Various other stains were tried out but proved to be less satisfactory.

In healthy young stems of *Arceuthobium*, the epidermis consists of a single layer of cells which is later gradually replaced by a secondary cuticularized layer without lenticels or stomata (Gill, 1935). The stomata of the young stem are so arranged that their longitudinal axes are at right angles to the longitudinal axis of the stem. Beneath this outer layer lies the cortical parenchyma enclosing 2 or more vascular strands. The latter may be grouped near the center, resembling a central cylinder, or are more or less scattered in the cortical parenchyma. There is no normal cork tissue in the stems.

The rupture of the outer cuticularized layer, thus directly exposes the thin-walled cortical parenchyma cells. The fungus eventually invades all tissues of

the central cylinder, excepting the vascular elements. In less advanced stages of infection only the outer cortical tissues are affected. Invading hyphae are intercellular (Pl. 5, fig. 3), growing between the cells and killing them. In well advanced stages the dead cells are greatly shrunken and rather inconspicuous, the space formerly occupied by them being filled with a profuse development of hyphae.

The mode of entrance of the parasite has not been demonstrated. Although specimens have been preserved at various intervals after inoculation, sections have failed to reveal germ tubes on the surface or penetrating the host. As stated elsewhere, there is a preponderance of lesions which appear to originate at the joints and at the base of the stems, indicating that entrance at these points is common. Examination of a number of sections of diseased and healthy stems revealed that the cuticularized epidermal layer, even in relatively old plants, is very thin in the region of the joint, which would facilitate penetration. Furthermore, the joints with their subtending scale-like leaves, as well as the area around the base of the stem, are ideal points for the accumulation of spores and moisture. However, entrance at other points is also indicated by the fact that lesions often occur at points midway between two joints. Microscopic examination of such lesions often failed to reveal any connecting mycelium between that point and the nodal region. In other such cases, however, intercellular mycelium was observed throughout the entire length of the internode. In the young stem, with a thin epidermal covering, penetration could presumably occur through the stomata. Later, when the protective covering of the stem is thicker and the stomates are absent, direct penetration in the internodal region seems doubtful, since no appressoria have been observed.

DISCUSSION

While several parasitic fungi are known which attack other plant parasites, a comparatively small number of them have been studied in detail and plant pathologists have made relatively few attempts to exploit the possibilities of biological control of plant diseases. Several fungi which attack other fungi parasitic on plants are known. A typical example is *Cicinnobolus cesati* De Bary which parasitizes certain of the powdery mildews and may prevent perithecial formation (Griffiths, 1899; Peterson and Johnson, 1928). *Tuberculina maxima* Rostr. attacks the pycnia of *Cronartium ribicola* Fischer and prevents the production of aeciospores. However, attempts to introduce this parasite into new areas have met with little success (Mielke, 1933; Hubert, 1935). Another parasite of *C. ribicola* and of *C. conigenum* Hedgc. and Hunt, *Fusarium bactridioides* Wr., has been introduced into Washington and Oregon in an attempt to control white pine blister rust, but has spread very slowly (Mielke, 1943). The importance of soil micro-organisms, including fungi, antagonistic to soil-borne plant pathogens has been more widely recognized in recent years, as pointed out in reviews by Waksman (1937) and Garrard and Lochhead (1938).

True mistletoes, of the genus *Phoradendron*, are attacked by a number of fungi (Seymour, 1929: 285; Weiss, 1941), few of which appear to be important path-

ogens. Wolf (1910) states that *Macrophoma phoradendri* Wolf may cause complete defoliation of *Phoradendron flavescens* Nutt. but that new growth forms again when the host resumes growth. Two recently described parasites of *P. flavescens* in California, *Protocoronospora phoradendri* Darling (Darling, 1940) and *Phyllosticta phoradendri* Bonar (Bonar, 1942), are said to be quite destructive to the host.

Pistillate flowers of *Arceuthobium* attacked by *Wallrothiella* do not produce seeds. Thus, in areas where it becomes established, this fungus reduces spread of the host. However, the parasite appears to be rather restricted by its moisture requirements and it is doubtful if it can be employed artificially for biological control purposes (Gill, 1935). The only other fungus described on *Arceuthobium* to date, *Metasphaeria Wheeleri*, has been reported only once and little is known concerning its effect on the host.

As previously pointed out, the anthracnose disease undoubtedly effects a considerable degree of biological control of *Arceuthobium* in areas where it is prevalent. This effect is particularly noticeable on *A. campylopodum* f. *cyanocarpum* and f. *microcarpum* in the Santa Catalina and Graham Mountains in Arizona and, to a more limited extent, on *A. campylopodum* f. *abietinum* and f. *divaricatum* in northern Arizona. Gill (1935: 220) noted that on *A. campylopodum* f. *tsugensis* in Washington, the disease had reduced pistillate plants bearing fruits to a minimum. The magnitude of such control is difficult to measure but there is little reason to doubt that local spread of dwarf mistletoe has been markedly reduced in these areas. It has been suggested (Bur. of Pl. Ind. 1940) that the fungus may offer some promise of usefulness as an agent of biological control in areas such as administrative and recreation sites, where cutting and pruning are undesirable. This possibility has been investigated only to a limited extent in the course of this study. An attempt was made in the fall of 1939 to establish the disease on healthy shoots of *A. douglasii* on a group of Douglas fir seedlings and saplings in the Sandia Mountains of New Mexico. In this experiment only a few positive infections resulted (See Table 3). It is believed that this failure was due largely to unfavorable environmental conditions prevailing at the time the inoculations were made, because other inoculation studies indicated that infection is more readily established in the spring or summer.

It is quite evident that *Septogloeum Gillii* is responsible for considerable control of dwarf mistletoe under natural conditions, but further studies will be necessary to determine whether or not its introduction into new areas for purposes of biological control would be practical.

SUMMARY

1. Dwarf mistletoe (*Arceuthobium*), an important parasite on conifers, is attacked by a hitherto undescribed imperfect fungus which causes an anthracnose and is responsible for the premature death of large numbers of shoots.

2. The disease has been found in six western states and occurs naturally on seven of the eight forms of *A. campylopodum* and on *A. douglasii*.

3. The fungus attacks primarily the stems, occasionally the fruits, of the mis-

tletoe plant, at first producing tiny yellowish-white spots which later become convergent and erumpent through the cuticularized epidermal layer, exposing large white spore masses. Pistillate plants are attacked more frequently than staminate ones.

4. The fungus is described as a new species, *Septogloeum Gillii*, and is characterized by the convergent character of the fruiting layer, the hyaline, continuous to 3-septate, cylindrical to fusiform, conidia, borne singly but repetitiously in great numbers at the tips of the rather long, often branched, conidiophores arising from a hyaline stromatic layer.

5. In artificial culture the fungus grows well, but very slowly, on most of the common agar media. Four strains have been differentiated.

6. The fungus is favored by a comparatively cool environment. The indicated minimum, optimum, and maximum temperatures for growth in culture are about 1.0°, 17.5°, and slightly above 22.5°C., respectively.

7. Observations indicate that the parasite is probably disseminated largely by rain and insects.

8. Inoculation tests demonstrated conclusively that *S. Gillii* is the causal organism and that infection is readily established on its natural hosts without the aid of wounds. It was also shown that when introduced through wounds it parasitizes *A. vaginatum* f. *cryptopodum* on which it has not been found in nature.

9. The fungus invades all internal stem tissues excepting the vascular elements and develops a profuse intercellular mycelium.

10. In some localities, the disease apparently greatly reduces the reproduction and local spread of its host and its possible use as an agent of biological control in certain restricted areas is suggested.

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EXPLANATION OF PLATES

PLATE 4

Fig. 1. *Arceuthobium campylopodum* forma *microcarpum* on spruce (*Picea engelmannii*) with numerous diseased shoots. × about ¾.

Fig. 2. Anthracnose symptoms on *A. campylopodum:* a, forma *cyanocarpum*, showing small covered lesions (left and center) and large confluent eruption of white spore masses (right); b, forma *tsugensis*, showing spore masses at joints; c, forma *microcarpum*, showing white spore masses along stem. a and b from dried material, × 2; c from fresh material, × about 2.5.

PLATE 5

Fig. 1. Development of fruiting layer of *Septogloeum Gillii* on *Arceuthobium campylopodum* forma *microcarpum:* a, covered; b, erupting; c, open; longitudinal sections, × 38; d, transverse section showing extensive continuous fruiting layer, × 24.

Fig. 2. Conidiophores and conidia of *S. Gillii* on *A. campylopodum* f. *microcarpum*, × 670.

Fig. 3. Transverse section through stem of *A. campylopodum* f. *microcarpum* showing intercellular hyphae of *Septogloeum Gillii* in cortical parenchyma, × 373.

PLATE 6

Fig. 1. Lesions on *Arceuthobium vaginatum* forma *cryptopodum* caused by *Septogloeum Gillii* following wound inoculation(a). Shoots wounded but not inoculated(b).

Fig. 2. Anthracnose lesions produced on *A. douglasii* following spore-suspension inoculation of non-wounded, healthy shoots; uninoculated control on right, × 4.

PLATE 4

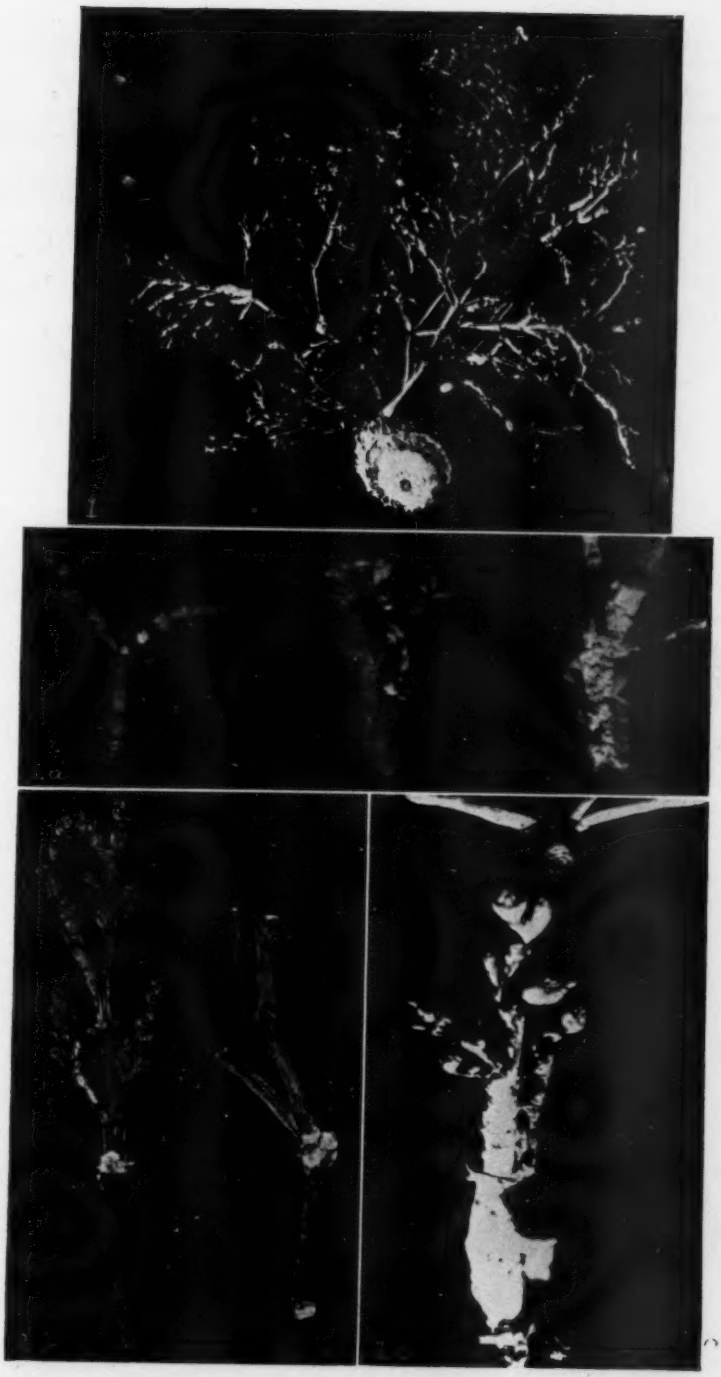
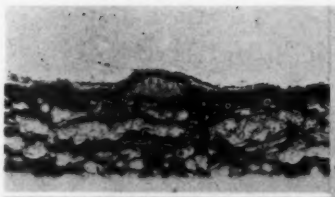


PLATE 5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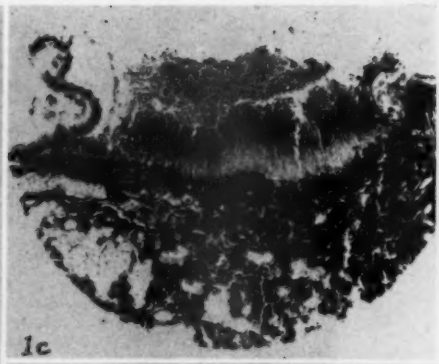
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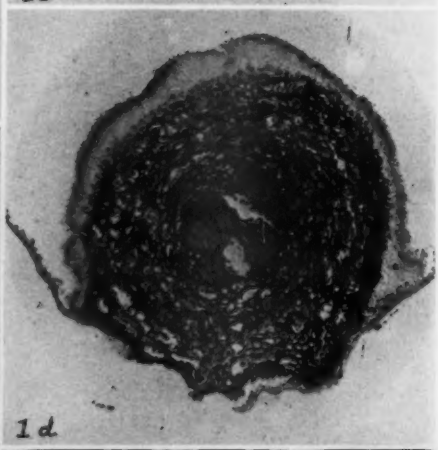
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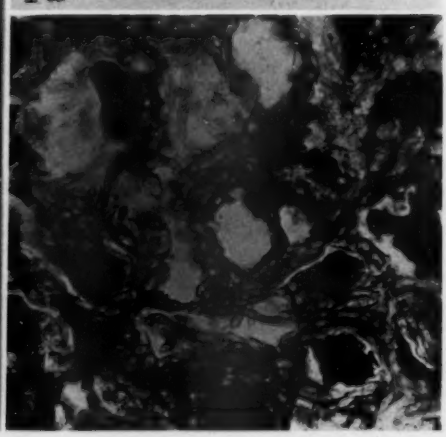

PLATE 6

ARCHEOLOGICAL DISCLIMAXES

By B. W. Wells

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In 1937 the writer (8) published in the Elisha Mitchell Journal a survey of 23 Southern Appalachian grass balds which lead to the conclusion that these grass and sedge communities were very old and had their origin in the local destruction of the high altitude forest and long continued use of the areas by the primitive or early hunter type of Indians. The late Cherokees with which the white men made contact were chiefly agriculturists. No attempt will be made here again to summarize the evidence for this theory except to point out that if fire, soil or climate factors were responsible, vast areas of the higher slopes would now be in the herbaceous condition.

Since this theory of early Indian origin of the grass balds was published Iverson (4) and Godwin (2) in Denmark and England respectively have propounded the idea that extensive heath areas of these countries go back to Neolithic man (2–3 thousand years B.C.) for their origin.

Iverson initiated the theory of forest destruction, land use and abandonment by stone age men, on the basis of pollen analyses. At the peat level which has been correlated with Neolithic time, he finds a sharp drop in tree pollen abundance which "express the vegetational developments in a region where land tilling people have occupied the land and cleared this dense primeval forest with axe and fire." The shift in non-tree pollen also supports his thesis. Especially significant is the sudden rise of certain weed pollens such as the plantains. The presence of charcoal is indicative of frequent fire over an extended period. Once cleared, Iverson believes the natives used fire so persistently to improve the terrain for cattle grazing that it was not until the early Iron Age many centuries later that the extensive heath (Calluna) areas of central Jutland came into existence as a response to the long time interference with the original forest. And once established the heath community was able to resist the reestablishment of the forest for reasons not yet entirely understood.

Godwin (3) finds that his extensive studies of peat profiles in the "Breckland" heath area of eastern England, definitely support the Neolithic origin hypothesis of Iverson.

The East Anglia heather had always been a major puzzle to ecologists and as Godwin states: "The basal question remained unanswered, whether this heathland is determined as such by natural factors or whether it represents the effect of human interference upon native woodland." Godwin concludes from his own large number of pollen spectra that: "There seems every reason for regarding these high values of non-tree pollens as witness of the origin of the Breckland heaths from a pre-existing vegetation of closed mixed oak forest. There is no direct evidence of the mechanism by which the vegetational change to heath was

brought about; but in view of the conclusions reached by Iverson, the correlation of this change with the Neolithic period must be noted." In a general way the heaths had their origin in Neolithic forest clearance.

Another example of a community initiated by man in prehistoric time and remaining intact to the present may be certain grasslands or savannas in New Guinea. Mr. Thomas L. Quay, former Naval Epidemic Disease Control Officer, called my attention to these grass dominated areas surrounded by tropical forest, the plant community giving every evidence of great age and of resisting reforestation. They are largely dominated by a grass called "kunai" or "alang-alang" by the natives, a heavy waist to head high bunch grass of the genus Imperata. As observed near Hollandia in the vicinity of Lake Sentani the areas dominated many of the rolling ridge tops. It was on one of these elevated savannas that Gen. McArthur had his New Guinea Headquarters at an altitude of approximately 1000 feet.

Archbold (1) describing the valley of the Crystal river in New Guinea refers to the "grass covered slopes, probably the result of native cultivation." Reed (7) describes these alang-alang or kunai grass areas and quotes the Australian forester, Lane-Poole (6) as follows: "On hilly slopes of dryer coastal region and in clearings of the rain forest, large kunai-covered plains occur in the great river valleys above high water mark. Many of these fields are thought to have supported primary forests which the natives have slowly cut away. The aboriginal method of fire hunting in these kunai areas acts as a further check on natural reforestation."

Lam (5) states: "The alang-alang fields are treeless, open and frequently very extensive. In the more thickly inhabited region they certainly occupy the greatest percentage of the land. Apparently they take over old cultivated terrains which finally through the loss of humus and through drying out have become valueless for crops and the alang-alang has hindered the growth of the young forest."

From the limited information available it would appear that these savannas present a non-forest community in a forest region which has been initiated by man centuries ago and which have without any purposeful aid of man, persisted to the present time.

In South America in addition to the well recognized climatic or dry season savannas are local grass areas distributed in the northern moist coastal countries which are surrounded by forest. The origin of these has usually been ascribed to the edaphic factor of excessive leaching. In the absence of proof of any edaphic theory, it is suggested that these puzzling herbaceous communities be rechecked from the standpoint of possible origin through the interference of prehistoric man.

The writer is fully aware of the necessity of much further study of all three of these persistent grass and shrub communities in forest zones, before final proof of their prehistoric human origin is gained. Enough evidence, however, is in hand, in the writer's judgment, to organize tentatively such communities under the name "archeological disclimaxes." Disclimax (disturbance climax) is Clement's term for a community initiated by man or animals.

SUMMARY

Three non-forest plant communities are reported from forested areas which are believed to have been initiated directly or indirectly by prehistoric men and to have persisted to the present. It is suggested that these be recognized under the name "archeological disclimaxes."

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TWO NEW TERRICOLOUS PHYCOMYCETES BELONGING TO THE GENERA LAGENIDIUM AND BLASTOCLADIELLA[1]

By Alma J. Whiffen

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Plate 7

The two new fungi herein described were both isolated from soil samples to which had been added water and pieces of boiled grass leaves as bait. The fungus which is to be described first was obtained from a sample of Cuban soil and is considered to be a new species of *Lagenidium* in the Lagenidiales. The other fungus was isolated from soil from Texas and is described as a new species of *Blastocladiella* in the Blastocladiales.

The leaf bait in the Cuban soil was overgrown by a species of *Pythium* in which the tips of the hyphae were swollen by an endobiotic parasite. The unicellular zoosporangial thalli of this parasite were similar in their appearance and in their method of zoospore discharge to those of *Olpidiopsis*. A careful examination of the resting body of this fungus revealed, however, the presence of an oospore, lying loosely in a vesicle to which the companion cell was attached. The structure of the resting body, therefore, indicated the relationship of this fungus to the Genus *Lagenidium*. This new species is described as follows.

Lagenidium Pythii n. sp.

Thallus intramatrical, causing hypertrophy of the hypha of the host. Zoosporangial thallus hyaline, smooth-walled, spherical to pyriform, 16–25 μ in shortest diameter. Zoospore ovoid, 2.1–2.8 x 3.5–4.2 μ, isocont, encysting on surface of the host hypha and discharging contents into the host through an evanescent penetration tube. Antheridial cell smooth-walled, spherical to ovoid, 8–13 μ in shortest diameter. Oogonium spherical to ovoid, smooth-walled, 12–23 μ in shortest diameter. Oospore spherical, smooth-walled, 7–15 μ in diameter.

Parasitic on *Pythium* sp., growing on grass leaf bait added to a sample of soil collected by Dr. Samuel B. Salvin, July, 1940, at Soledad (Cienfuegos), Cuba.

Thallo intra matricem; zoosporangio unicellulari, hyalino, sphaerico vel pyriformi, 16–25 μ in diametro minimo; muro levi. Zoosporis ovoideis, 2.1–2.8 x 3.5–4.2 μ, isocontis. Antheridio sphaerico vel ovoideo, 8–13 μ in diametro minimo; muro levi. Oogoniis sphaericis vel ovoideis, 12–23 μ in diametro minimo; muro levi. Oosporis sphaericis, 7–15 μ in diametro; muro levi.

[1] These studies were made at Harvard University during the tenure of a National Research Council Fellowship. The author wishes to thank Dr. William H. Weston Jr. for his interest in this study and Dr. Frederick K. Sparrow Jr. for reading and criticizing the manuscript of this paper.

The zoospore of *Lagenidium Pythii* may germinate without coming into contact with the hyphal wall of its host. In this case, the development of the fungus is arrested after the formation of a germ tube but the germ tube may branch several times before its development ceases. Therefore, germination of the zoospore of *L. Pythii* is not dependent upon a thigmotropic response to the living host.

The germ tube from a zoospore which is in contact with its host penetrates the hyphal wall and once within the hypha, the germ tube expands while the contents of the encysted zoospore gradually disappear. It would seem that in the early stages of the germination of the zoospore, prior to the establishment of a parasitic relationship with its host, the young parasite utilizes for growth its own reserve of oxidizable material within the zoospore. Subsequent enlargement of the parasitic thallus with concomitant swelling of the host results in the early disruption of the connection between the zoospore cyst and the young thallus and shortly thereafter the cyst can no longer be seen attached to the hyphal wall.

The zoosporangial thallus in growing to maturity passes through successive stages in which the refractive globules increase in number and become uniformly dispersed; the small vacuoles throughout the protoplasm coalesce into one large central vacuole; and the zoosporangial wall gradually thickens. These stages in the development of the zoosporangium are the same as those already adequately described for species of *Lagenidium* and *Olpidiopsis*.

The mature zoosporangium of *L. Pythii* is unicellular and spherical in form with a single exit tube (Fig. 12). Cleavage of the zoospores occurs within the zoosporangium and they are completely formed at the time of their discharge from the zoosporangium. As they emerge from the exit tube, the zoospores accumulate in a spherical mass at the mouth of the tube and remain quiescent until the emptying of the zoosporangium is completed. There is no evidence of a restraining membrane about the spore mass and just prior to the dispersal of the zoospores the flagella of the peripheral spores can be seen thrashing about freely. The zoospores are biflagellate and measurements made on stained preparations of the zoospores reveal that the flagella are of equal length. No cystospores were found during the study of *L. Pythii* and it is, therefore, assumed that the zoospores of this parasite are monoplanetic.

The resting bodies and the zoosporangia of *Lagenidium Pythii* may develop in the same swelling of the host hypha (Fig. 6) or a single swelling may be filled only with resting bodies (Fig. 14). The thalli of incipient resting bodies and zoosporangia cannot be differentiated in their early stages of development. The adjoining of two thalli and the subsequent increase in the quantity of refractive material in their protoplasm is the only means by which a young resting body may be identified (Fig. 9) as such. One of the paired thalli enlarges much more rapidly than the other one and this thallus becomes the oogonium into which the smaller or antheridial thallus is drained through an opening in the contingent walls. The process of plasmogamy is accomplished without the formation of a fertilization tube. During plasmogamy the protoplasm within the oogonium

begins to contract and becomes invested with a membrane which later thickens as the oospore matures (Fig. 13). The oospore thus lies free within the oogonium.

It should be noted that *L. Pythii* is the first species of *Lagenidium* to be described as parasitizing a fungus. All other species of *Lagenidium* are parasitic in algae, mosses, *Potamogeton*, rotifers, crab eggs, or copepods. The identity of the species of *Pythium* which is the host of *L. Pythii* has not been determined. Its zoosporangia are of the inflated, lobulate type with filamentous evacuation tubes (Fig. 11), and its sex organs consist of an antheridium which arises from the hypha near the oogonial stalk and an oogonium which is almost completely filled by its oospore (Fig. 8). The average diameter of the oogonium is 18μ and of the oospore 12μ.

The fungal parasite of *Pythium* described in this paper is placed in the Genus *Lagenidium* because of the structure of its resting body. The one character which the species of *Lagenidium* have in common and which distinguishes *Lagenidium* from *Olpidiopsis* is the development of an oospore which lies free within the oogonium. The species of *Lagenidium* show no agreement among themselves in the characters relating to the number of cells in the thallus, the locus of spore cleavage, and the behavior of the zoospore. For instance, although exogenous cleavage of the zoospores as in *Pythium* is generally recognized as typical of *Lagenidium*, actually only fifty-two per cent of the described species, in which the manner of zoospore cleavage is known, show any degree of constancy in regard to this character, exhibiting consistently exogenous cleavage of their zoospores. The placing of *L. Pythii* in *Lagenidium* brings to four the number of species in this genus which are characterized by endogenous zoospore cleavage. In four other species the zoospores may be but partially delimited in the zoosporangium and the maturation of the zoospores is completed externally or as in *L. Oedogonii* the cleavage of the zoospores may be either completely exogenous or completely endogenous. The manner in which the zoospores are cleaved is unknown in five doubtful species of *Lagenidium*. Therefore, despite the resemblance of its zoosporangial phase to that of *Olpidiopsis* and the anomalousness of its zoospore discharge in respect to *Lagenidium*, it is to be concluded that on the basis of the structure of its resting body *L. Pythii* must be assigned to *Lagenidium* rather than to *Olpidiopsis*. However, if the oogonium of this species were to be filled completely by its oospore, then the resting body in its form and simplicity would be indistinguishable from the typical resting body of *Olpidiopsis*. One is thus led to believe that *L. Pythii* may be a transitional form connecting *Olpidiopsis* and *Lagenidium*.

Couch and Whiffen (1942) have described a species of *Blastocladiella, B. cystogena*, which is characterized by the absence of a zoosporangial phase and the presence of gametangial cysts in the life cycle. The primary zoospores upon emerging from the germinating resting body, encyst as gametangia from each of which are discharged four isogamous gametes. The Blastocladiaceous fungus which was isolated from the sample of Texan soil has the same type of cyst-producing life cycle as *B. cystogena* but differs from this previously described

species in having a smooth-walled resting body and much smaller gametangial cysts and gametes. This new species of *Blastocladiella* receives its specific name from the small size of the cysts.

Blastocladiella microcystogena n. sp.

Thallus of resting sporangium sessile or stalked; spherical to ovoid, 12–68 μ in diameter; wall of resting sporangium smooth, hyaline to light yellow brown, 1.3–4.5 μ thick. Germination of resting sporangium by cracking open of wall and formation of one exit papilla, through which uniflagellate zoospores are discharged. Zoospores encysting almost immediately; encysted zoospore (gametangium) spherical, 4.8–6.2 μ in diameter; each gametangium discharging four uniflagellate gametes, 2.5 x 2.9 μ, which fuse in pairs. Zygote biflagellate, encysting and germinating to form a plant bearing a resting sporangium.

On grass leaf bait added to a sample of soil collected by Dr. John N. Couch and Philip Couch, December 28, 1941, at Terrell, Texas.

Sporangiis perdurantibus sessilibus aut stipitatis, sphaericis vel ovalibus, 12–68 μ in diametro; muro levi, hyalino vel aureo-fusco, crasso 1.3–4.5 μ; germinatis uniflagellatis zoosporis emissis qui in sporas immotas se transformant et gametangia faciunt. Gametangia sphaerica, 4.8–6.2 μ in diametro; horum quodque quattuor cellulas sexuales emittit 2.5 x 2.9 μ, quae binae se coniungunt. Zygotis biflagellatis, sporangiis perdurantibus formatis per transformationem in sporas immotas et germinationem.[2]

The mature resting body of *B. microcystogena* has a pale yellow wall the outer surface of which is completely smooth. The whole of the resting body of this fungus appears to be markedly translucent, due to the pale color of the wall and the smallness of the widely dispersed globules of reserve food material. Only the wall of the resting body is pigmented; the protoplasm and the oil globules are colorless. The thallus in which the resting body is borne may be stalked but is more frequently sessile.

Germination of the resting body is accomplished by the cracking open of the outer wall and the emergence of an exit papilla (Fig. 2). The zoospores are delimited within the resting sporangium and are extruded in an irregular mass at the mouth of the exit papilla. These zoospores, each of which has a single flagellum, are capable of only limited motility and soon after being discharged they encyst. Within an hour after encystment four small gametes are discharged from each cyst (Fig. 4). These gametes fuse in pairs and the zygote, after a period of motility, germinates by the production of a germ tube and the body of the zygote is then transformed directly into the resting body thallus (Fig. 3), which matures within a week.

At the present time the "cystogenes" type of life cycle is known to occur in two species of *Blastocladiella*, two species of *Allomyces*, and in the species of *Catenaria* recently transferred by Couch (1945) from the Chytridiales to the Blastocladiales. Indeed, of the genera now included in the Blastocladiaceae only in the type genus, *Blastocladia*, has the cyst-forming type of life cycle not as yet been found.

[2] The Latin diagnoses were prepared by Mr. Harrison A. Nelson.

SUMMARY

Two new species are described. The first species, *Lagenidium Pythii*, is characterized by olpidoid zoosporangia and sexual thalli consisting of a small male cell attached to a larger female cell within which a single, free-lying oospore is borne. This is the only species of *Lagenidium* known to be parasitic on a fungus.

The second new species, *Blastocladiella microcystogena*, has the same "cystogenes" type of life cycle as is found in *Blastocladiella cystogena* but differs from this species in the smoothness of the wall of its light yellow-colored resting bodies and the smallness of its gametangial cysts and gametes.

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EXPLANATION OF PLATE 7

Fig. 1. Mature resting sporangium of *Blastocladiella microcystogena* attached to an epidermal leaf cell. × 360.

Fig. 2. Germinated resting sporangium of *B. microcystogena* with primary zoospores encysted at mouth of the exit tube. × 360.

Fig. 3. Young thallus of *B. microcystogena*. × 620.

Fig. 4. Gametangia and one gamete of *B. microcystogena*. × 620.

Fig. 5. Gametangia and gametes of *Blastocladiella cystogena*, drawn for comparison with Fig. 4. × 620.

Fig. 6–14. *Lagenidium Pythii*.

Fig. 6. Resting body and zoosporangia in the same swelling of the host. × 840.

Fig. 7. Early stage in the development of the zoosporangia. × 500.

Fig. 8. Oogonium and antheridium of the host of *L. Pythii*. × 70.

Fig. 9. Early stage in the development of the resting bodies. × 500.

Fig. 10. Germination of zoospores of *L. Pythii* on hypha of *Pythium* sp. × 500.

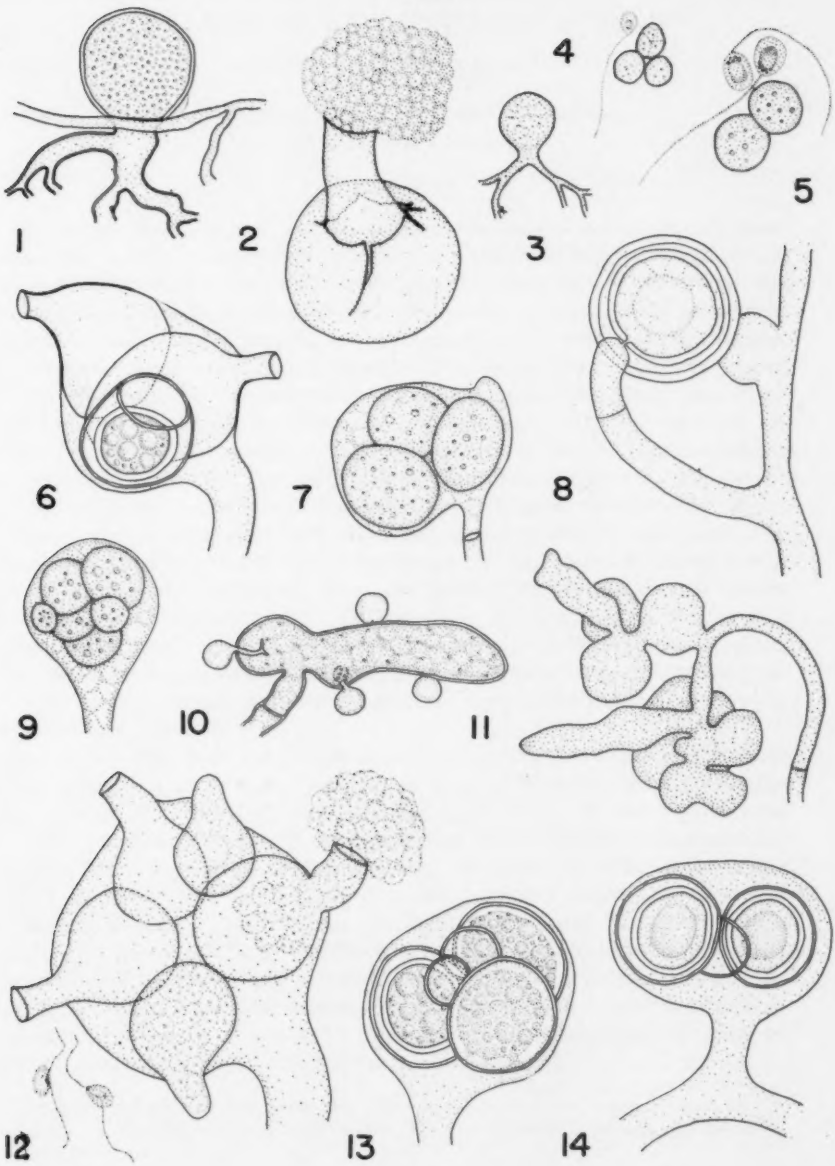
Fig. 11. Zoosporangium of the host of *L. Pythii*. × 70.

Fig. 12. Zoosporangia: prior to cleavage of zoospores, after cleavage of zoospores, and after discharge of zoospores. × 840.

Fig. 13. Three resting bodies showing stages in the maturation of the oospore. × 840.

Fig. 14. Mature resting bodies. × 840.

PLATE 7



THE WOUNDING EFFECTS OF SMALL HIGH-VELOCITY FRAGMENTS AS REVEALED BY HIGH-SPEED RADIOGRAPHY*

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Plates 8–10

The technic for making radiographs with conventional x-ray equipment makes it necessary to use exposure times ranging from the order of a second to several minutes in duration. Obviously, such long exposures do not permit making radiographs of rapidly moving objects. Recently, however, x-ray equipment has become available which allows a radiograph to be made with an exposure time of the order of one-millionth second. This equipment has been developed by the Westinghouse Company and has been described by Ehrke and Slack (1941) and more recently by Slack and Thilo (1944). With such a short exposure time, it is now possible to make radiographs of various types of rapidly moving objects. As early as 1940, Slack published pictures showing some of the phenomena which could be demonstrated by high-speed radiographs. These included a club striking a golf ball, a shot-gun charge passing through wood, etc. The technic was immediately taken over by government research laboratories to be used in the field of ballistics. Slack and Thilo (1944) discuss some of the applications of the technic to this field and show pictures of such objects as a projectile moving down the barrel of a gun and projectiles piercing armor plate. Other ballistics laboratories in this country and abroad used the technic extensively but due to the confidential nature of these investigations, no mention can be made of this work.

The technic has been used with great success in the Princeton Biological Laboratories as a part of an extensive program of research dealing with the mechanism of wounding by small high-velocity missiles. It has proved to be extremely valuable in studying the behavior of animal tissues during and immediately after the passage of these missiles. Some of the earlier observations made with this technic are contained in the papers of Harvey, Butler, McMillen and Puckett (1945); Butler, Puckett, Harvey and McMillen (1945); Puckett, Grundfest, McElroy and McMillen (1946) and Puckett, McElroy and Harvey (1946). These earlier experiments have dealt primarily with the wounding effects of small steel spheres. The materials to be covered in this paper represent an extension of this work to cover the wounding effects of small irregular fragments, as revealed by microsecond radiographs.

*The work reported in this paper was done under a contract, recommended by the Committee on Medical Research between the Office of Scientific Research and Development and Princeton University.

METHODS

Living cats, under deep Nembutal anaesthesia, have been used in all of the experiments. Shots were made into the tissues of the thighs and abdomen.

Missiles used in the experiments were small steel fragments with masses ranging from 300 to 600 mg. Certain of these fragments were of 75-mm. or 3-inch shells, obtained from government arsenals. In other cases, fragments were made from sections of small wire nails. The fragments were mounted by wooden sabots in standard 30-caliber cartridge cases and fired from a specially constructed test gun. The fragments were fired at velocities averaging 3000 ft./ second.

Radiographs were made with the Westinghouse Micronex Unit. The reader is referred to the paper of Slack and Thilo (1944) for a complete description of this unit. It consists essentially of a Westinghouse surge generator and a special x-ray tube. Discharge of a bank of condensers in less than a microsecond supplies a current of several thousand amperes to the tube. The voltages used in these experiments ranged from 180 to 240 KV.

The generator is triggered by the missile either making or breaking an electrical circuit. By the use of a delay circuit, the interval between the time the circuit is triggered and the actual discharge through the x-ray tube can be varied from a few microseconds to several milliseconds. This makes it possible to obtain a microsecond radiograph at any desired time during or immediately after the passage of a missile through a part of the animal body.

EXPERIMENTAL

Earlier experiments (Harvey et al, 1945) have shown that a small high-velocity steel sphere passing through the thigh of a cat or dog, produces a temporary explosive cavity within the tissues. This cavity is many times larger than the sphere or the permanent cavity left after the passage of the missile. The cavity, at first, conical in shape, expands rapidly and, at its maximum size, assumes the shape of a prolate ellipsoid. The maximum temporary cavity formed in the thigh of a cat after the passage of a $\frac{4}{3}\frac{1}{2}$-inch steel sphere with an impact velocity of 4600 ft./second is shown in the microsecond radiograph in figure 1. The radiograph was made 300 microseconds after the sphere struck the thigh. The sphere which produced this cavity had passed out of the field when the radiograph was made but, for comparison, a sphere of this size, taken from another radiograph, has been included in the upper right of this figure.

The expansion of this cavity is extremely rapid, taking place in approximately 1/3000 of a second. After the cavity reaches a maximum size, it collapses and the thigh undergoes secondary pulsations before returning to normal size.

The temporary cavity can be explained by the fact that a high radial velocity is imparted to the tissues by the missile. This causes the tissues to move away from the missile path at high velocities,—at a speed approximately 1/10 that of the velocity of the missile. In addition to this type of stretching and tearing of relatively soft muscle and connective tissues, nerves may be stretched, bones broken and small blood vessels ruptured as a result of the rapid expansion of the

cavity. The formation of this large temporary cavity gives a reasonable explanation of the seemingly abnormal amount of damage produced by these small high-velocity missiles.

Quantitative studies (unpublished data) have shown that the volume of the temporary cavity produced by a small high-velocity steel sphere is proportional to the energy delivered to the tissues by the sphere. In the case of an irregular fragment, the amount of energy lost to the tissues will depend not alone on the energy of the fragment but also on the projected cross-section area of the fragment as it passes through the tissues. Thus, an elongate fragment which strikes the tissues broadside and passes through them with this orientation, will lose more energy to the tissues and will produce a more serious wound than a similar fragment which passes through oriented along its long axis and presenting less of its surface area to the tissues. It is obvious that if a fragment changes its orientation in passing through the tissues, the amount of energy delivered at any one point will be dependent on the orientation of the fragment at this particular point. Since the size of the temporary cavity is dependent on the energy delivered, a fragment which changes its orientation in traversing the tissues will produce a temporary cavity whose shape is irregular and quite unlike the rather symmetrical cavities produced by spheres. It follows from this that a study of the configuration of the temporary cavity will give an accurate picture of any changes in orientation of the fragment as it traverses the tissues. These facts can be demonstrated by the series of microsecond radiographs to be presented below.

Figure 2 is a microsecond radiograph of the thigh of a cat which was struck by a small fragment of a 75-mm. shell. The mass of the fragment was 630 mg. and its striking velocity 3000 ft./second. The radiograph was made 250 microseconds after the fragment struck the thigh. The fragment struck broadside and emerged with the orientation shown in this figure. The cavity is very large at the point of entry and much smaller at the point of exit of the fragment. The femur was struck directly by the missile and has been badly shattered. This cavity should be compared with a similar one produced by a $\frac{4}{11}$-inch steel sphere and shown in figure 1.

A second case is illustrated by the microsecond radiograph shown in figure 3. In this case, the left thigh of a cat was struck by an elongate fragment made from a small wire nail. The fragment was 11 mm. in length, 2.5 mm. in diameter and had a mass of 380 mg. Its striking velocity was approximately 3000 ft./second. The radiograph was made 257 microseconds after the fragment struck the thigh. The fragment has emerged from the thigh and is shown at the extreme right of the figure. Yaw cards placed at the points of entrance and exit of the missile, show that the fragment changed its orientation only slightly in traversing the tissues, hence the striking similarity of this cavity to that formed by a sphere.

Large temporary cavities, similar to those described in the thigh, are also formed when a missile traverses other parts of an animal body such as the head or abdomen. The rôle of the temporary cavity in head wounding has been described by Butler, Puckett, Harvey and McMillen (1945). The temporary

cavities produced in the abdomen by high velocity steel spheres are described in a recent paper by Puckett, McElroy and Harvey (1946). Due to its greater thickness, the abdomen is a more favorable region than is the thigh for a study of the behavior of irregular fragments. The following radiographs will show something of the nature of the temporary cavities formed in the abdomen of cats by irregular fragments.

Figure 4 is a microsecond radiograph of the abdomen of a cat, made 350 microseconds after it was struck by a small fragment of a 75-mm. shell whose striking velocity was 3000 ft./second. The dimensions of the fragment were 8.5 x 4 x 3 mm., its mass 410 mg. Yaw cards show that the fragment struck the abdomen broadside and emerged with the orientation shown in this figure. The irregular shape of this cavity confirms the fact that the fragment changed its orientation in traversing the abdomen. Striking broadside, it created the large cavity, with an accompanying bulge of the abdominal wall, seen in the left of the radiograph. Near the center of the abdomen, it apparently turned more nearly on its long axis, veered up, to emerge at the angle shown here. It should be noted that this cavity had not reached its maximum size when the radiograph was made.

A temporary cavity of approximately maximum size is shown in figure 5. This radiograph was made 350 microseconds after the abdomen was struck by a small fragment made from a wire nail. The dimensions of the fragment were 12.5 x 2.5 mm. The mass of the fragment was 415 mg.; its striking velocity 3000 ft./second. A photograph of a fragment of approximately this size has been inserted in the lower right of this figure.

Temporary cavities, similar in nature to those produced by spheres and fragments, are also formed after the passage of standard types of ammunition such as a 22-caliber bullet. If the projectile traverses the tissues oriented along its long axis, the cavity is symmetrical in configuration; very similar to that formed by a steel sphere. If, on the other hand, the bullet wobbles or, in any way, is deflected during its passage through the tissues, the cavity becomes irregular in outline and very much like that formed by a fragment which changes its orientation.

The microsecond radiograph in figure 6 shows a 22-caliber-long bullet just after it emerged from the abdomen of a cat. This bullet has a mass of 2.68 grams and struck the abdomen with a velocity of 1100 ft./second. The bullet apparently passed through the abdomen without a change in its orientation, as the outline of the cavity is symmetrical. The cavity has just begun to expand and, at its maximum size, will have a diameter about twice that shown in this figure.

The temporary cavity plays an important rôle in abdominal wounding. The extremely rapid expansion of the cavity may be likened to an explosion within the abdomen. Obviously, structures directly in the path of the missile are severely damaged. In addition, the "explosion" blows apart the visceral organs, causing extensive tears in the mesenteries and severe rupturing of the smaller blood vessels.

In addition to damage due to stretching and tearing, secondary damage can result from rapid pressure changes which accompany the development of the cavity. The nature of these pressure changes has been discussed by Puckett et al (1946). More recently, actual measurements of these pressures have been made by piezzo-crystal gauges (Harvey et al, unpublished data). It has been found that the large temporary cavity is a partial vacuum, since air cannot move in quickly enough to maintain atmospheric pressure. This short period of lowered pressure can have serious effects on tissues if gas is present. Autopsy studies have revealed multiple perforations of the intestine at points well removed from the missile track. It seems likely that the suddenly lowered pressure around the intestine is the cause of these perforations. The intestine simply explodes at points where gas pockets are present.

The materials presented above are designed primarily to point out the extreme value of high-speed radiography in a study of the mechanism of wounding. The ability to photograph tissues during and immediately after the passage of a missile through them is a significant advance in the study of the manner in which these missiles produce their damaging effects.

SUMMARY

1. The application of microsecond radiography to a study of the mechanism of wounding by high-velocity missiles is described.

2. Microsecond radiographs show that a temporary explosive cavity is formed in animal tissues immediately after the passage of a high-velocity missile. This cavity is many times larger than the missile which created it or the permanent cavity left after the passage of the missile.

3. A comparison is given of the nature of the cavities produced by steel spheres, irregular fragments and standard ammunition.

4. The rôle of the temporary cavity in the wounding mechanism is briefly discussed.

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EXPLANATION OF PLATES

Fig. 1. Microsecond radiograph of the thigh of a cat showing the maximum temporary cavity formed after the passage of a $\frac{4}{5}$-inch steel sphere whose striking velocity was 4600 ft./second. The radiograph was made 300 microseconds after the sphere struck the thigh. A sphere of this size is shown in the upper right of the figure.

Fig. 2. Microsecond radiograph of the thigh of a cat showing the temporary cavity produced by an elongate fragment of a 75-mm. shell. The fragment, shown emerging from the thigh, had a mass of 630 mg. and a striking velocity of 3000 ft./second. The radiograph was made 250 microseconds after the fragment struck the thigh.

Fig. 3. Microsecond radiograph of the thigh of a cat showing the temporary cavity produced by an elongate fragment made from a small wire nail. The fragment, seen at the extreme right of the figure, was 11 mm. in length, 2.5 mm. in diameter and had a mass of 380 mg. The impact velocity of the fragment was 3000 ft./second. The radiograph was made 257 microseconds after the fragment struck the thigh.

Fig. 4. Microsecond radiograph of the abdomen of a cat showing the temporary cavity produced by a small fragment of a 75-mm. shell. The fragment, seen just emerging from the abdomen, had a mass of 410 mg. and a striking velocity of 3000 ft./second. Its dimensions were $8.5 \times 4 \times 3$ mm. The radiograph was made 350 microseconds after the fragment struck the abdomen.

Fig. 5. Microsecond radiograph of the abdomen of a cat showing the maximum temporary cavity formed after the passage of an elongate fragment made from a small wire nail. The dimensions of the fragment were 12.5×2.5 mm. The mass of the fragment was 415 mg. and its striking velocity 3000 ft./second. A fragment of approximately these dimensions is shown in the lower right of this figure.

Fig. 6. Microsecond radiograph of the abdomen of a cat showing the expanding temporary cavity formed after the passage of a 22-caliber long bullet. The projectile, which had a striking velocity of 1100 ft./second is seen just after emerging from the abdomen. The temporary cavity has just begun to expand and is not at its maximum size.

PLATE 8

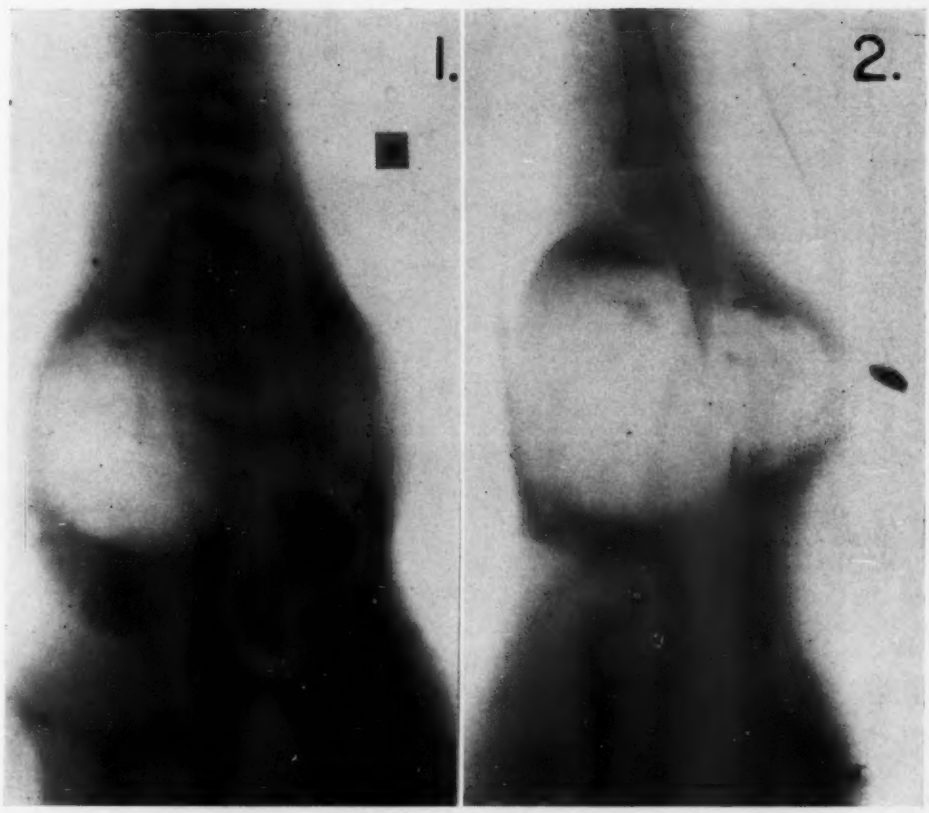


PLATE 9

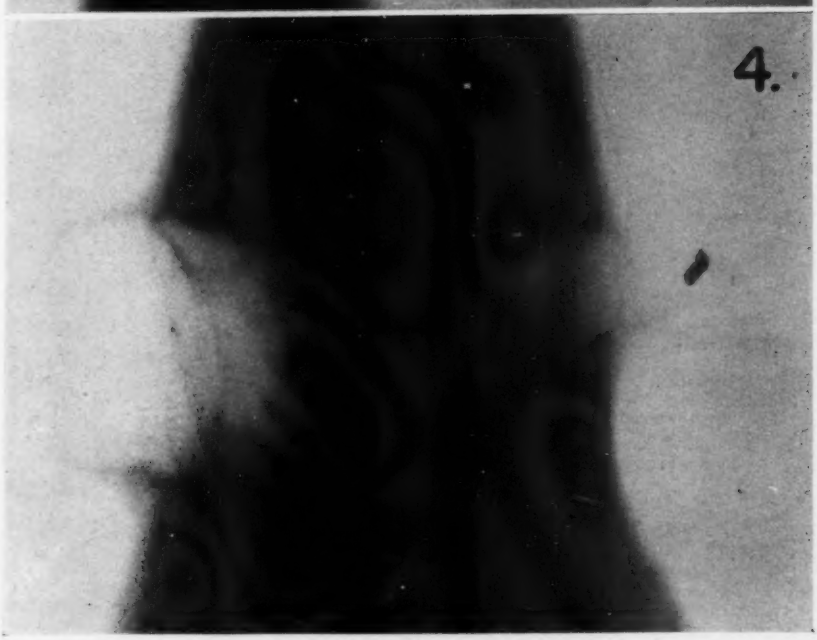
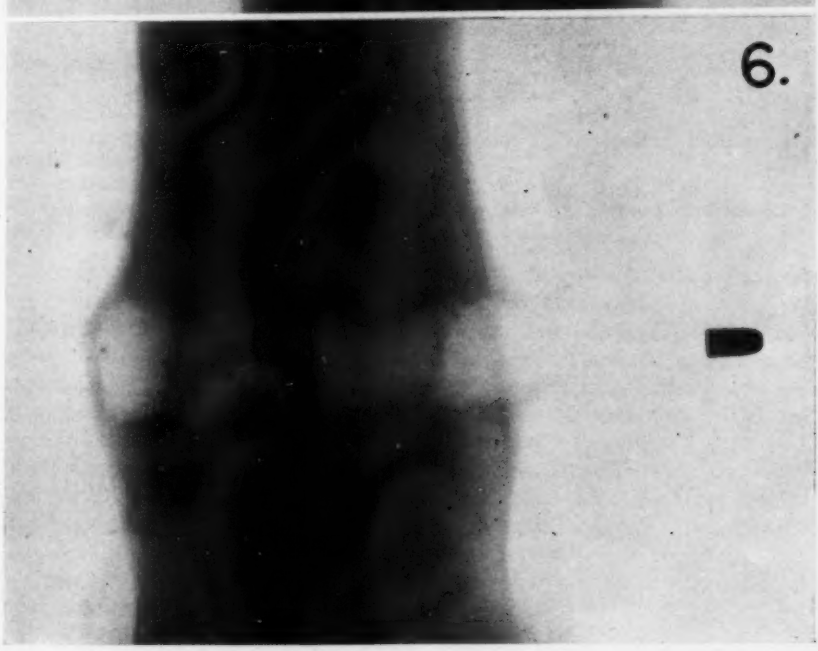


PLATE 10



NEW OR RARE HETEROBASIDIOMYCETES FROM NORTH CAROLINA—II

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Plates 11–14

The present paper describes some species of lower Basidiomycetes collected by the author in the vicinity of Chapel Hill, North Carolina, during a search for new or rarely found fungi in this group. This is a continuation of the report begun in a previous issue of the Journal of the Elisha Mitchell Scientific Society (**60:** 17–26. 1944), and records the finding of a number of fungi, none of which, with the exception of a single species, have previously been reported in our area. The finding of *Stypella minor* Möller gives us our first record of this genus in North Carolina. Further collections of *Tulasnella* and *Gloeotulasnella* bring the total number found by the author up to 6 species, none of which had been previously reported in the Southeastern States.

All collections of species described here were made during the early spring months of 1944. The majority of our saprophytic Heterobasidiomycetes seem to thrive and fruit best during the cooler months of winter and early spring.

Platygloea peniophorae Bourd. & Galz. Bull. Soc. Myc Fr. **25:** 17. 1909.
Plate 11, figs. 1–9

Mature basidia transversely 3-septate, 4.4–5.5 x 21.4–28.2 μ; basidiospores ovate, somewhat flattened on one side, apiculate, 4.7–5.8 x 6.9–8.3 μ. Conidia rather abundant, catenulate, obovate or oval, borne separately from the basidia or sometimes on the same hypha, 3.9–5.3 x 7.3–12.6 μ. Clamp connections abundant, particularly in basidial and conidial formation.

The fungus was growing along with *Tremella* sp. within the pustules of *Dacryomyces minor* Pk, and therefore had no definite fructification of its own. *Platygloea peniophorae* has been reported on *Peniophora* and *Gloeocystidium*, but there appears to be no earlier record of it on *Dacryomyces*. There was nothing in the external appearance of the little *Dacryomyces* pustules to indicate that the *Platygloea* was present. A few haustorium-like branches were found which had applied themselves to the hyphae of the *Dacryomyces*.

Martin, in his recent taxonomic review, "The Tremellales of the North Central United States and Adjacent Canada" (U. Iowa Stud. Nat. Hist. **18:** No. 3, 88 pp. 1944), records *Platygloea peniophorae* from Tennessee, Iowa, Oregon, Quebec, Ontario, and Europe. This is the first report of it in North Carolina.

Growing within the fructifications of *Dacryomyces minor* Pk. on an old decorticated branch of sycamore. Battle Park, March 23, 1944.

Tremella sp.

Plate 13, figs. 1–15

Haustorial branches present on the hyphae, usually with characteristic double clamp connections at their bases. Basidia subglobose to obovate, sometimes with clamp connections, mostly 4-celled, frequently 2-celled, 10.7–13.7 x 13.3–18.3 μ, often proliferating from the bases of other basidia; basidiospores obovate to nearly globose, apiculate, 5.8–7.8 x 8.7–10.7 μ, germinating by repetition, or producing small, almost globose conidia.

Here, as in the case of the previously discussed species, the fungus occurs entirely within the small yellow pustules of *Dacryomyces minor* Pk., without altering the appearance of the latter. In some of these pustules the *Platygloea* and *Tremella* are found together; in others they occur separately. There is little doubt that the *Tremella* is parasitic, since haustorial threads extending from peculiar branches with double clamp connections, are frequently found wrapped around the hyphae of the *Dacryomyces*.

The present fungus agrees in some ways with the descriptions of *Tremella tuberculariа* Berk. The latter has been described as growing out of the ostioles of perithecia of sphaeriaceous fungi, probably as a parasite. The basidial measurements are given by Martin as 12–16 x 15–20 μ, while the spores are said to be subglobose to globose and 7–8 x 7.8–9 μ. It is obvious that the measurements of the basidia and spores of our fungus are very close to these. The spores of our fungus, however, tend to be obovate to subglobose, rather than globose. Martin reduces Whelden's species, *Sebacina globospora* Wheld. (Rhodora **37:** 121. 1935), to synonymy with *T. tuberculariа* Berk. The author has examined a type slide of Whelden's fungus, sent from the Farlow Herbarium by Dr. David Linder, and finds that the present fungus agrees rather closely with ours in size of basidia and spores.

Our fungus differs significantly from previously described specimens of *T. tuberculariа* in its parasitism of *Dacryomyces minor*, rather than a sphaeriaceous fungus, and in its habit of growth entirely within the fructifications of its host, thus having no distinct form of its own. We are not yet certain whether the characteristics of this fungus are sufficiently different to allow it to be considered an undescribed species, or whether its similarities to *T. tuberculariа* are strong enough to ally it simply as a variety of that species.

Growing within fructifications of *Dacryomyces minor* Pk. on decorticate sycamore branch. Battle Park, March 23, 1944.

Tremella encephaliformis Willd. Magaz. f. d. Botan. **2**(4): 17. 1788.
Tremella encephala Willd. ex Pers. Syn. Method. Fung., p. 623. 1801.
Naematelia encephala Fries. Syst. Myc. **2: 227.** 1822.
Tremella encephala Bref. Untersuchungen Gesammt. Myk. **7**(2): 127. 1888.
Naematelia encephaliformis (Willd.) Coker. Jour. Elisha Mitchell Sci. Soc. **35:** 137. 1920.

Plate 12, figs. 1–16

Fructifications creamy white, pulvinate, arising singly as cushionlike swellings and pushing through the bark of dead oak branches, measuring 2–5 x 5–12 mm. and 2–4 mm. high, with a firmly gelatinous or almost cartilaginous hymenial layer inclosing a fleshy white center; shrinking only slightly on drying and becoming hard, nodulated, yellowish or tan bodies.

Clamp connections abundant along the hyphae and at the bases of the basidia; basidia 2-3-4-celled, with 2-celled forms very common, irregularly septate, globose to conspicuously elongate, 12.2–16 x 13.7–18.3 (−30.5) μ, sterigmata 33–137 μ long; basidiospores subglobose to almost globose, 7.8–11.3 x 9.7–12.8 μ, germinating by repetition or budding out globose to obovate conidia. Spore print white. Conidia also produced on special segments, or conidiophores, at the ends of some of the hyphae and from some of the basidia. Conidia about 3.2–3.6 x 4–6.2 μ.

As can readily be seen from the above description and from the illustrations, this specimen is quite variable as to the size of its basidia and spores. Moreover, the 2-celled basidia are about equal in number to the 4-celled ones, and the septa vary in arrangement from vertical to diagonal or even horizontal. Also it seems that almost any cell in the gelatinous hymenium is capable of budding out conidia, but this phenomenon may be stimulated by very favorable moisture and temperature conditions.

From the standpoint of nomenclature, the fungus has had a very confusing history. The author has reviewed Willdenow's original description in the *Magazin für die Botanik* and found, as Coker did earlier, that Willdenow named the fungus *Tremella encephaliformis*, rather than *Tremella encephala* found in most of the literature. Persoon, in 1801, incorrectly copied the name in his *Synopsis Methodica Fungorum*, and this apparently accounts for the almost universal misinterpretation of the specific name by other authors from that time on. Fries, in 1822, studied this plant and decided to place it in his new genus, *Naematelia*. He therefore called it *Naematelia encephala* Fries. In 1888, Brefeld studied the plant from the standpoint of conidial formation by the basidiospores. Since there was a profuse production of globose conidia of typical *Tremella* type, he returned the fungus to the genus *Tremella* and called it "*Tremella encephala* (nov. spec.), früher *Naematelia encephala* Wilden.," apparently thinking that Willdenow had originally described it as a *Naematelia*. The correct specific name did not appear again until Coker, in 1920, called the fungus *Naematelia encephaliformis* (Willd.) Coker. Since *Naematelia* is no longer considered a valid generic name, we at long last return for the correct name to Willdenow's original terminology.

Bresadola (Ann. Myc. **6**: 46. 1908) described a specimen of *Tremella encephaliformis* on dead oak branches in Moravia and called it *T. encephala* (Willd.) Bref. var. *Steidlerii* Bres. This had basidia measuring 14–16 x 16–18 μ, basidiospores 8–9 μ in diameter, and conidia 3 x 3–4 μ. Now Brefeld, as has already been pointed out, showed earlier that his specimen on pine had basidiospores which produced abundant conidia. Moreover, the measurements of basidia and basidiospores of Bresadola's fungus are about the same as those given for typical specimens on pine. Therefore, there remains only one distinguishing

feature—its occurrence on oak—and this would certainly not constitute sufficient reason for considering it a valid variety. We do not think that our specimen on oak differs in any essential way from those described on pine.

Coker reports the earlier finding of this species in our area by Curtis and by Schweinitz. In both cases the fungus occurred on fallen pine branches.

Growing on old fallen oak branches in a woody bog. April 12, 1944.

Stypella minor Möller. Protobasidiomyceten, p. 77. 1895.
Plate 11, figs. 19–24

Fructifications very small, soft-gelatinous, white, gangliform, evanescent on drying, reviving partly when moistened, no clamp connections present; paraphyses conspicuous, freely branched, somewhat contorted. Basidia subglobose to ovoid, 7.8–9.2 x 10.7–13.1 μ; basidiospores subglobose to somewhat elongate ovoid, apiculate, 4.9–5.3 x 6.8–8.7 μ, germinating by repetition.

Martin has reduced to synonomy with *Stypella minor* Möller the fungus described by Linder (Mycologia **25:** 105. 1933) as *Tremella gangliformis* Linder, the specific name of which is certainly descriptive of the plant. Although quite small and inconspicuous, the fungus can readily be recognized when collected by its gangliform appearance, as Dr. Linder has so adequately described and illustrated; that is, it is composed of little white pustules connected with each other by white strands of the same texture.

The only other species described in this genus is *Stypella papillata* Möller. The genus is considered distinct from *Tremella* on the basis of its byssoid nature and the presence of a coarse, dry subiculum. The latter, if present at all in our fungus, must be quite ephemeral, as it was not observed in either of our two collections. This appears to be the first report of the genus in the Southeastern States, although it is said to be rather widespread.

Collected twice on elm wood, once in a woody bog along New Hope Creek, March 28, 1944; again in a brush pile on the edge of Sparrow's pasture, April 15, 1944.

Sebacina sublilacina Martin. Mycologia **26: 262.** 1934.
Plate 11, figs. 10–18

Effuse, thin, waxy-gelatinous, grayish when first collected, becoming decidedly lilaceous, drying to an inconspicuous film, no calcareous granules observed, paraphyses rather large, generally branched, forked at the tips. Cystidia fairly abundant, thin-walled, long-cylindrical or clavate, usually tapering towards the apex, 5.4–11.7 x 27–55 μ. Basidia subglobose, 8.7–9.7 x 9.7–10.7 μ; basidiospores reniform or flattened on one side, 4.4–4.9 x 8.7–9.7 μ.

Basidia and spores average a bit larger in our fungus than in the description given by Martin for the species. However, in other important respects the fungus agrees well with the latter both in its microscopic appearance and its general appearance to the naked eye.

Growing on very rotton, decorticated deciduous wood, probably oak. Battle Park, March 13, 1944.

Tulasnella violacea (Johan-Olsen) Juel. Bih. Svensk. Vet.-Akad. Handl. **23,** Afd. 3(12): 22. 1897.

Plate 14, figs. 19–27

Effuse, thin, waxy, somewhat warty in appearance under a lens, color gray to grayish lavender when fresh, drying to a light pinkish bloom or a conspicuous lilaceous color. Hyphae mostly parallel to the substratum, 3.9–6.8 μ in diameter, without clamp connections. Basidia varying greatly in shape from broadly obovate to clavate, often irregular in shape, 7.7–11.2 x 9.7–14.6 μ; epibasidia 7.0–7.7 x 9.7–11.7 μ; basidiospores curved, subfusiform, obliquely attenuated towards the apiculus, 5.1–6.3 x 9.2–14.6 μ, germinating by repetition.

This specimen fits well the earlier descriptions of the species. It has not been previously reported from the Southeastern States, although it is said by Martin to be quite common in Ontario and Iowa, and occurs also in New England, California, and Europe.

On fallen limb of a deciduous tree, growing on the bark. Battle Park, March 22, 1944.

Gloeotulasnella calospora (Boud.) Rogers. Ann. Mycologici **31**: 201. 1933.
Tulasnella calospora (Boud.) Juel. Bih. Svensk. Vet.-Akad. Handl. **23,** Afd. 3(12):23. 1897.

Plate 13, figs. 16–20

Effuse, thin, soft-gelatinous, varying from dark, almost bluish gray to light tan, almost invisible on drying. Hyphae without clamp connections; gloeocystidia absent. Basidia with globose heads and elongate stalks, 7.8–10.7 x 14.6–23.4 μ; epibasidia at first subglobose, later becoming obovate to fusiform, 5.8–8.3 x 8.7–15.6 μ; basidiospores long and narrow, almost straight to distinctly arcuate, 2.9–4.1 x 14.6–21 μ, sometimes germinating to produce small secondary spores.

Gloeotulasnella calospora has apparently been found previously in this country only in Iowa, Maine, and Oregon. We have found it only once at Chapel Hill.

Growing over the surface of an old resupinate pore fungus on decaying wood. Deciduous woods behind Kenan Stadium, April 18, 1944.

Gloeotulasnella traumatica Bourd. & Galz. Bull. Soc. Myc. Fr. **25**: 32. 1909.
Gloeotulasnella opalea Rogers. Ann. Mycologici **31**: 198. 1933.

Plate 14, figs. 1–18

Effuse, 190–370 μ thick, surface wavy and uneven, waxy-gelatinous, cloudy hyaline to muddy brown, sometimes violet tinted, looking much like a thin, brown *Sebacina*. Hyphae with abundant clamps; gloeocystidia irregularly distributed, usually embedded in the deeper layers of hyphae and therefore not generally found along with the basidia, very variable in size and shape, obovate to elongate and cylindrical or capitate, often curved and irregular in outline, hyaline at first, becoming yellow, 7.6–23 x 24.4–107 μ. Hymenium compact, with hyphae mostly perpendicular to the substratum, basidia typically obovate to clavate-capitate, often with well-defined stalks and frequently with elongate sub-basidial pedicel hyphae, basidia measuring 6.8–9.2 x 9.7–19.4 μ; epibasidia generally

obovate, 4.4–5.8 (−7.5) x 5.8–8.7 (−15) μ; basidiospores subglobose to obovate, 4.4–5.8 x 5.8–7.8 μ, germinating by repetition.

This fungus appears to have been found previously in our hemisphere only in Ontario and Iowa. The present collections were made at several different times during the early spring from the same spot.

Growing on the underside of a large fallen limb of sycamore, covering an area about 2–5 inches in breadth and 1.5 feet in length. Battle Park, February to April, 1944.

EXPLANATION OF PLATES

PLATE 11

(All figures × 1183)

Platygloea peniophorae (Figs. 1–9).

Fig. 1. Hyphae with basidium and conidia, occurring along with basidia of *Dacryomyces minor*.

Fig. 2. Basidiospores.

Figs. 3 and 4. Conidial formation.

Figs. 5–8. Germination of basidia.

Fig. 9. Haustorial branch applied to *Dacryomyces* hypha.

Sebacina sublilacina (Figs. 10–18).

Fig. 10. Probasidium.

Fig. 11. Young septate basidium.

Fig. 12. Germinating basidium.

Figs. 13 and 14. Paraphyses.

Figs. 15–17. Cystidia.

Fig. 18. Basidiospores.

Stypella minor (Figs. 19–24).

Fig. 19. Probasidium.

Figs. 20–22. Germinating basidia.

Fig. 23. Basidiospores, two of which are producing secondary spores.

Fig. 24. Paraphysis.

PLATE 12

Tremella encephaliformis (Figs. 1–16).

Fig. 1. Vertical section through the fructification, showing the fertile outer gelatinous layer and the sterile inner spongy layer. × 7.

Fig. 2. Two-celled basidium germinating. × 720.

Figs. 3 and 4. Basidia, showing irregular arrangement of septa. × 720.

Fig. 5. Group of basidia. Note the irregular arrangement of septa in the majority of basidia. × 720.

Fig. 6. Basidiospores. × 1183.

Fig. 7. Hyphae, showing fusion and clamp connections. × 720.

Fig. 8. Irregular, 3-celled basidium. × 720.

Fig. 9. Two-celled basidium after germination. × 720.

Fig. 10. Germinating 4-celled basidium. × 720.

Fig. 11. Basidiospores germinating, one giving rise to a secondary basidiospore, the others producing conidia. × 720.

Fig. 12. Conidium producing a secondary conidium. × 1183.

Figs. 13 and 14. Basidia budding out conidia. × 1183.

Fig. 15. Conidiophore-like hyphae producing conidia. × 1183.

Fig. 16. Branched hypha with young probasidia. × 720.

PLATE 13

(All figures × 1183, except where indicated.)

Tremella sp. (Figs. 1–15).

Figs. 1 and 2. Probasidia.
Fig. 3. Four-celled basidium beginning to germinate.
Fig. 4. Top view of 4-celled basidium.
Fig. 5. Basidium and probasidia.
Fig. 6. Intermixed hyphae and basidia of *T.* sp. and *Dacryomyces minor*. × 822.
Figs. 7–9. Haustorial branches applied to the hyphae of *Dacryomyces minor*. Note the characteristic double clamps.
Figs. 10 and 11. Two-celled basidia.
Fig. 12. Abnormal basidial development.
Fig. 13. Basidium with four cells almost in a row.
Fig. 14. Basidiospores, some germinating to produce secondary spores.
Fig. 15. Basidiospores producing conidia.

Gloeotulasnella calospora (Figs. 16–20).

Fig. 16. Hypha with probasidia.
Fig. 17. Probasidium and young basidium.
Fig. 18. Basidium with fully developed epibasidia.
Fig. 19. Basidium with germinating epibasidia.
Fig. 20. Basidiospores, one of which has produced a small secondary spore.

PLATE 14

(All figures × 1183, except where indicated.)

Gloeotulasnella traumatica (Figs. 1–18).

Fig. 1. Basidium and probasidia, supported by sub-basidial pedicel cells.
Figs. 2–4. Development of basidia.
Fig. 5. Hyphae with clamp connections.
Fig. 6. Group of probasidia and germinated basidia.
Figs. 7–9. Basidia germinating.
Fig. 10. Basidium with two epibasidia.
Figs. 11–16. Gloeocystidia. (Fig. 14, × 720.)
Fig. 17. Abnormal gloeocystidium which apparently began its development as a basidium. Walls thick due to gelatinization.
Fig. 18. Basidiospores, two of which are germinating to produce secondary spores.

Tulasnella violacea (Figs. 19–27).

Figs. 19 and 20. Probasidia.
Figs. 21–25. Basidia in various stages of germination. Note variations in shape.
Fig. 26. Basidiospores, two of which are germinating to produce secondary spores.
Fig. 27. Hyphal fusion.

PLATE 11

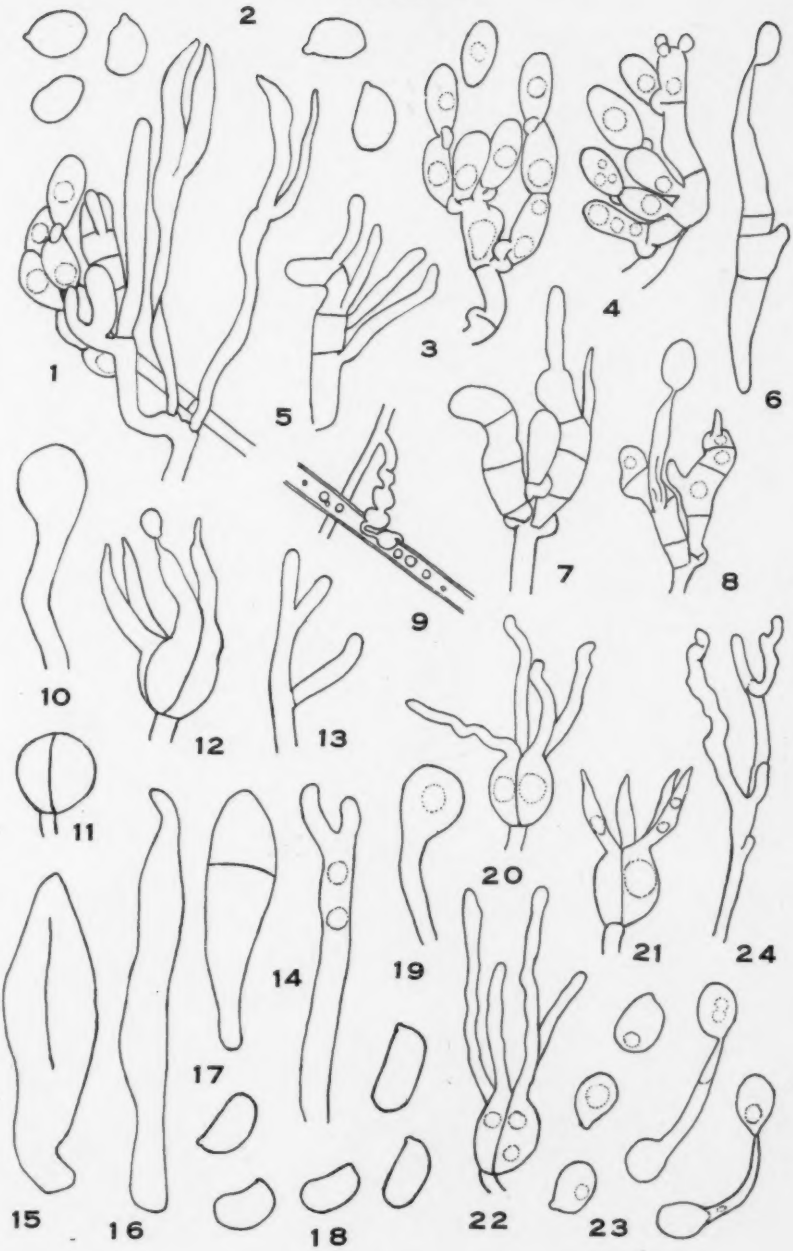


PLATE 12

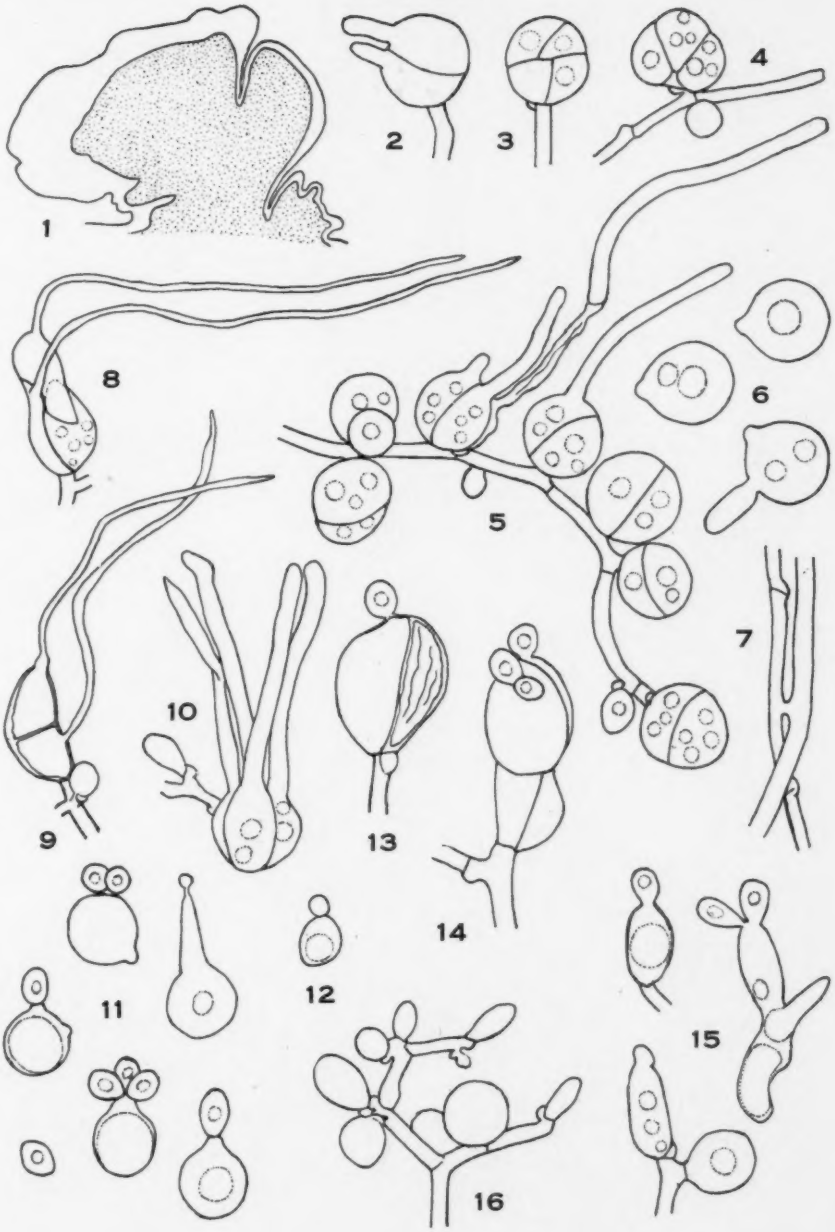


PLATE 13

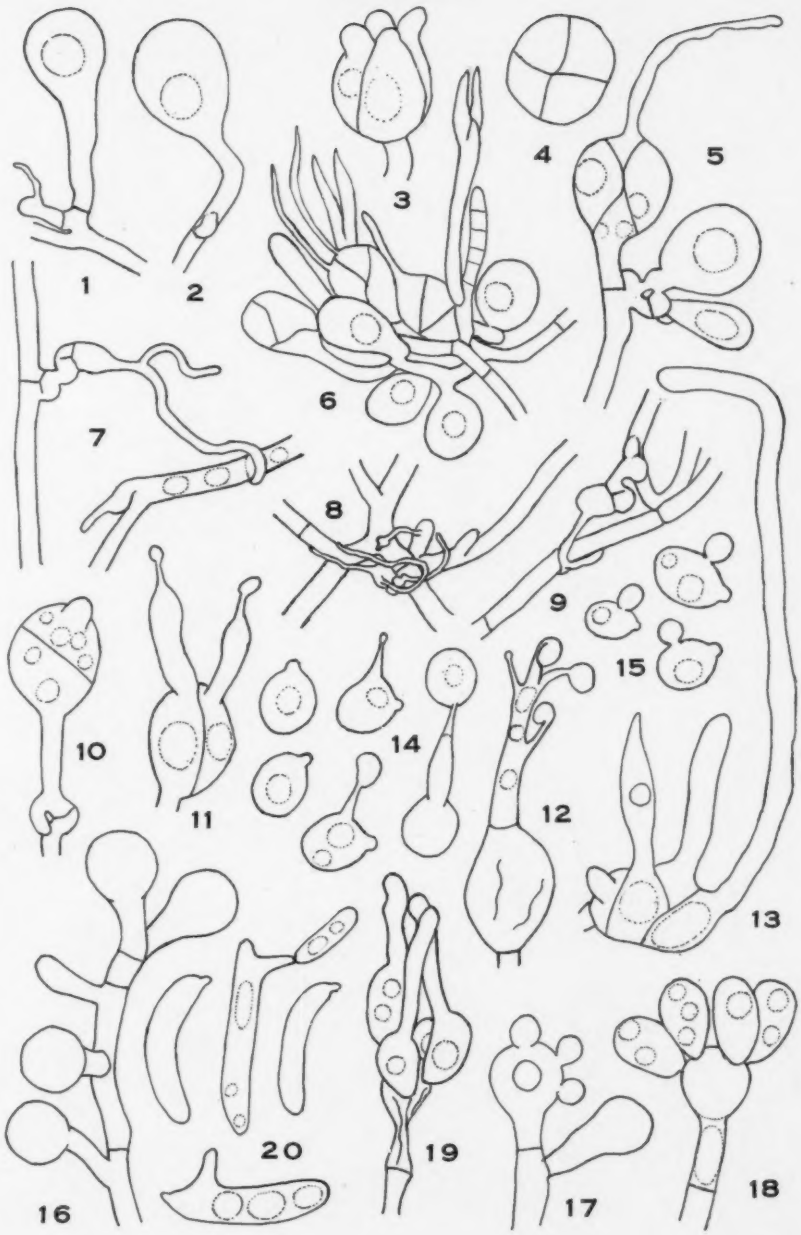
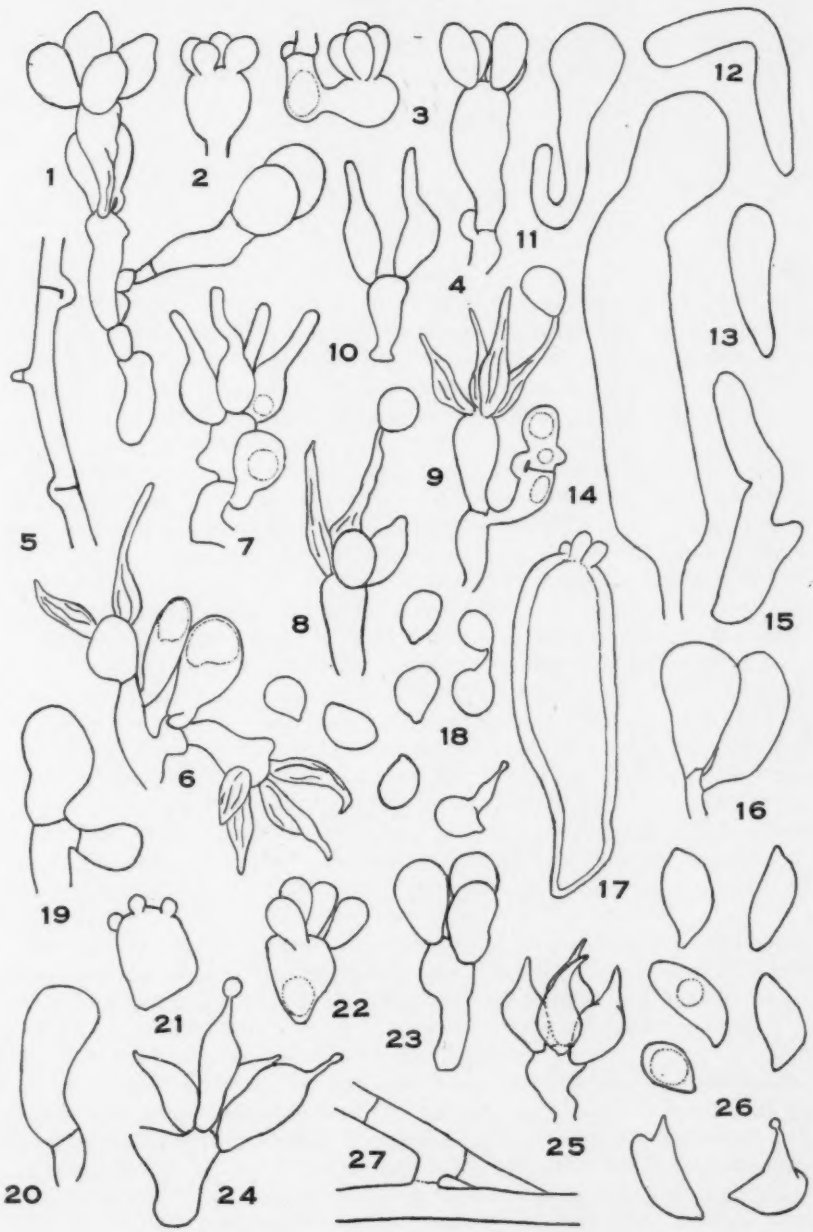


PLATE 14



AN ALBINO RUSTY DAB, LIMANDA FERRUGINEA, WITH NOTES ON OTHER ABNORMALITIES IN FLATFISHES

By E. W. Gudger

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One Text Figure

This specimen was taken by a commercial fishing boat on November 18, 1944, in about 20 fathoms in the coastal waters somewhere between Block Island and Montauk Point. It was landed at Stonington, Connecticut, that afternoon and came into New York next morning in a large shipment of fishes consigned to Beekman Fillets Company, 214 Front Street. It is impossible to locate the boat that took the fish and the captain thereof, nor can the place of capture be more narrowly noted than above.

In sorting the fishes in the shipment, this albino dab came to light and was sent to Mr. Wm. C. Neville of the Fish and Wild Life Service, 155 John Street. He, being on the lookout for rarities for us, telephoned to ask if I would like to have this interesting specimen. The answer was a prompt affirmative, and a messenger was at once sent for it. To Mr. Neville and to Beekman Fillets Company, my best thanks are herewith tendered.

The specimen was received at about 4 p.m. and, when freed from the wrappings of damp cloths, was perhaps the most beautiful fish I have ever seen. The upper surface was as pure white as was, and is, the lower, but underneath the white was a lovely pink due to the fact that the whole complex of blood vessels was visible through this transparent veil of skin. All who saw this unique specimen were so interested and excited that no one noted whether or not the eyes were pink. By the time everyone had looked the fish over, it was too late to have it photographed. So it was laid on a piece of smooth board and wrapped carefully in cloths, to prevent warping or twisting while immersed in alcohol over night. Next morning it was photographed as may be seen in Figure 1.

Press of other work has postponed the description of this specimen until now. At this writing, after nearly four months in alcohol, the fish measures 10 inches in standard length and 12 over all. The body is 4.4 inches wide between bases of median fins. The weight today is 6 ounces. This is a small specimen. In our waters it is known to reach 21.75 inches in length.

The rusty dab, like the other flatfishes, is an abnormal fish when comparison is made with all other fishes. But, as a member of the order Heterosomata or Flatfishes, it is entirely normal. Paradoxically it is a normally abnormal fish.

When a flatfish is very young it swims like any other fishlet with its dorsoventral axis vertical, and it has an eye on each side of its head. It is a normal little fish, and if it continued to swim vertically each side would develop color alike. But it shortly lies down on one side and is notable for a lack of coloration

on that side. The side it lies on is very definitely fixed for certain genera of flatfishes—in *Limanda* it is the left side. Indeed only one reversed *Limanda* seems ever to have been recorded (by Duhamel du Monceau in 1777). And as our little fish takes on this prone position in life, the color develops on the right side, the eye of the left side migrates across the forehead and comes to rest on the right, upper, or colored side. The lower side, having lost its eye, also fails to develop any color. Our dab has become a normal flatfish, but is fundamentally an abnormal fish.

FIGURE 1. AN ALBINO RUSTY DAB, LIMANDA FERRUGINEA, TAKEN OFF BLOCK ISLAND NOVEMBER 18, 1944

HOW VARIOUS ABNORMALITIES MAY ARISE IN FLATFISHES

In growing up there are a number of ways in which our little fish could, from the standpoint of his tribe, have become abnormal.

(1) Due to lie on its left side with its head pointing to the right as is usual for Limandas, it might have settled down on its right side with its head pointing to the left. Whereupon the left side would have developed color and the right eye would have migrated to this left side, while the right side would have become blind and colorless. Such a flatfish is labelled reversed, i.e., the sides have been "swapped" and the head points in the wrong direction. Such a left-pointing dab would be reversed and would be an abnormal dab.

(2) The next abnormality has to do with the eye. The little fish settles down on its left side, as is the rule for dabs, and the left eye begins its migration to the upper side of the head. But if it stops on the middorsal line of the head, or sometimes if it gets barely across it so that, holding the little dab up blind side to one's eye, one can see the eye just across the dorsal ridge, there will generally be an overhanging hook formed of the bases of the anterior fin rays. Here is a remarkable abnormality—which, however, is almost always, if not surely, tied up with abnormal coloration on the underside.

Now we are come to that abnormality of which there are four varieties—coloration. With the little dab resposing normally on its left side, it may go wrong in two degrees in its coloration of each side.

(3A) It may develop few or many separate patches of color on its under, white, or blind side. Such an abnormal fish is denominated partially ambicolorate, partially colored below as it is above. Such a dab is abnormal.

(3B) If, however, our dab goes on to develop total coloration on the under side, it becomes a totally ambicolorate dab, with both sides colored alike, eye generally totally or partially rotated across the forehead, and with an overhanging hook. Such a flatfish is about as abnormal, as grotesque, as these normally abnormal flatfishes can become.

Even now our little dab has still left two ways of becoming abnormal. Lying on its left and colorless side, with the left eye safely and normally emplaced on the upper or right side, it may still take one of two wrong paths.

(3C) It may develop white areas about on its normally dark upper side. Such a dab will be called a piebald or a partial albino. There are varying degrees or stages of partial albinism ranging up to the next deformity.

(3D) The dab may fail to develop any color on the upper side and become a total albino. Total or perfect albino dabs or other flatfishes are probably rather rare, as are total ambicolorates, called "black bellies." The intermediate stages of partial ambicoloration and of albinism in flatfishes are fairly common.

When our little dab came, it seemed to be a perfect albino, but close examination of the upper surface brought to notice certain slight discolorations, which were at first thought to be bits of dirt. But closer examination revealed these as "token" rusty spots of the normal coloration. There is one behind the right eye, and a bit of dark tissue shows at the edge of the operculum. On the hinder part of the body are faint discolorations. Such areas are stronger on the bases of the caudal rays and more distinct on the hinder half of the caudal fin. Then some of the tips of the hinder dorsal and anal rays are a bit dark. Possibly these "token" darkenings are accentuated by the solvent action of the alcohol on the oils in the skin. These small discolorations forbid the calling of this fish a perfect albino, but it certainly is an excellent example of an albino dab.

Most noticeable is a dark bar extending from the front of the left or rotated eye forward to the middle point of the upper jaw. This apparently is more or less common for albino dabs. Such is portrayed (more accentuated) in an albino *Limanda limanda* in Figure 16 of the late J. R. Norman's great "Monograph of the Flatfishes (Heterosomata)," London, 1934, p. 23.

Despite these small discrepancies, our little fish is a beautiful specimen of an albino rusty dab. Ambicoloration in varying degrees is not uncommon among dabs. In his "Monograph" (p. 23), Norman says that of 51 ambicolorate flatfishes of 6 groups examined by him 9 specimens were dabs. Total albinos (or total white ambicolorates) among flatfishes are rare since, like our specimen, "Even in the more completely albino examples there is nearly always some pigment on the head on the ocular side, generally extending from the tip of the snout backwards to about the region of the preoperculum, and complete absence of pigment on this surface is very rare indeed." Albino fishes are "sports" and, according to Norman, "The percentage is perhaps higher in the Heterosomata [Flatfishes] than in any other group of fishes." Flatfishes being ab-

normal to begin with, albinism seems to come more easily for them than for forms ordinarily normal.

With regard to the cause of albinism in flatfishes, I can do no better than to refer the reader to Norman, who in the general part of his "Monograph", devoted 7 pages to a section on "Albinism, Ambicoloration and Reversal." He states that the literature dealing with the abnormalities of coloration of flatfishes is an extensive one. Then in addition to the references in the general part of his book, he refers specifically to 15 articles by 12 men, and says that these should be particularly consulted with reference to these abnormal coloration phenomena in flatfishes. But he does not review these theories of albinism, nor does he set forth one of his own. If Norman, in the greatest work ever published on the flatfishes, keeps silent as to the reputed causes of albinism in such fishes, I think that I can safely follow his example.

A THREE-YEAR TRIAL OF HYBRID POPLARS IN NORTH CAROLINA*

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The observations contained in this report cover a period of only three years, an interval which at first glance may seem too brief for an adequte evaluation, but events have made necessary the time limitation, and the results of the experiment seem indicatively, if not conclusively, valid enough to publish. The experiment was unfortunately terminated by the destruction of all the trees during a logging operation on an adjacent tract.

The program was to include a cytological study of the chromosome numbers and behavior in conjunction with a taxonomic study, and the further crossing of promising species or hybrids as indicated.

From *a priori* considerations, the South with its longer growing season, adequate moisture and soils, its abundant sub-marginal agricultural land and its need for more effective soil conservation would seem to be the ideal place for the growth of hybrid poplars. That such considerations, while plausible, are not without error, the following report will indicate.

MATERIALS AND METHODS

A total of one thousand and nine cuttings of sixty-seven hybrids, selections and pure species of *Populus* were planted in rows in planned random at intervals of six feet between trees and eight feet between rows. The trees were planted in three sites, two of which were contiguous and differed only in the fact that one field had been in cultivation the previous year and from which a crop of soy beans had been taken. The soil of this field was free of grass and not infested with weeds. The contiguous field contained a mixture of grasses, but could not be called a sod. The soil of both fields could be described as a sandy loam. A third smaller planting including many of the hybrids was made on a hillside in a heavy red clay which was deficient in organic matter and had suffered considerable sheet erosion. Survival and growth were so poor on this site that the survivors were removed and the land used for other purposes at the end of the second year. It should be mentioned, however, that this soil was in cultivation up to the time of planting the trees and that corn at least could and did grow on it.

Of the materials used in this study, cuttings of fifty-nine of the selections which are listed first in the following pages were made available to the author by the kindness of Mr. Phelps Vogelsang, Research Forester of the Dow Chemical Company of Midland, Michigan. For the last eight listed selections I am indebted to Dr. E. Chalmers Smith of the Biological Laboratories of Harvard University.

*Part of a program in Forest Genetics supported by a grant from the General Education Board.

13P39	Populus nigra var. italica x P. canadensis	
15	Sport called Northwest hybrid.	
16	Populus nigra x P. laurifolia	
17	" " x " "	
18	" " x " "	
20	" angulata x P. berolinensis	
20P39	" deltoides x P. canadensis	
21	" nigra var. charkowiensis x P. eugenii	
22	" sargenti x P. berolinensis var. rossica	
23	" " x " "	
24	" tacamahaca var. candicans x P. berolinensis	
25	" maximowiczii x P. trichocarpa	
26	" tacamahaca var. candicans x P. berolinensis	
27	" nigra var. charkowiensis x P. caudina	
28	" petrowskyana x P. caudina	
30	" maximowiczii x P. berolinensis	
30P39	" sargenti x P. deltoides	
31	" nigra x P. laurifolia	
32	" maximowiczii x P. berolinensis	
34	" " x P. plantierensis	
38	" nigra x P. trichocarpa	
39	" rasumowskana x P. caudina	
40	" charkowiensis x P. "unidentified."	
41	" nigra var. betulifolia x P. trichocarpa	
42	" suaveolens	
44	" charkowiensis x P. caudina	
47	" robusta	
48	" canadensis erectus	
52	Populus charkowiensis x P. plantierensis	
55	" incrassata	
56	" caudina	
57	" fastigeata x P. or var? sorbieriens??	
59	" unidentified sport	
64	" balsamifera var. virginiana x P. berolinensis	
65	" maximowiczii x P. balsamifera var. virginiana	
66	" nigra x P. trichocarpa	
67	" maximowiczii x P. trichocarpa	
69	" angulata x P. berolinensis	
71	" charkowiensis x P. berolinensis	
72	" nigra x P. laurifolia	
73	" " x P. berolinensis var. rossica	
74	" szechuanica	
75	" maximowiczii x P. trichocarpa	
76	" nigra x P. laurifolia	
77	" maximowiczii x P. plantierensis	
78	" nigra x P. laurifolia	
81	" " x P. trichocarpa	
82	" maximowiczii x P. berolinensis	
83	" " x " "	
87	" nigra baatanicorum-vitrum x P. trichocarpa	
88	" charkowiensis x P. balsamifera var. virginiana	
91	" " x P. caudina	
93	" " x P. berolinensis	
94	" " x P. trichocarpa	

95	"	angulata x P. incrassata
96	"	sargenti x P. berolinensis var. rossica
97	"	petrowskyana x P. caudina
98	"	maximowiczii x P. "
99	Populus	rasumowskyana x P. incrassata
1P42	"	trichocarpa var. hastata x P. koreana
4P42	"	" " " " x P. laurifolia
5P42	"	" " " " x P. nigra var. italica
11P42	"	" " " " x P. tacamahaca var. michauxii
15P39	"	deltoides x P. nigra
18P39	"	balsamifera var. virginiana x P. cuminata
38P38	"	tacamahaca x P. simonii
69P38	"	maximowiczii x P. nigra

RESULTS

Our records do not include individual records for each selection, but the tallest measured tree was thirty-eight inches and the smallest fourteen inches, and only four trees in the entire planting died. At no time in their brief existence did any of the trees look vigorous. During the sustained warm weather of mid-summer, there was considerable leaf curl and defoliation, usually followed by a partial recovery and new leaves in the cooler weather of the fall. Soil drainage of the field was only fair and it is possible that the trees suffered somewhat the first year from excessive moisture. It seems clear, however, that poor site or cultural practices did not account for all of the observed results.

The inhibiting effect of grass and weeds upon growth of hybrid poplars and hard woods in general has recently been emphasized by Schreiner (2). Essentially the same information pertaining to hybrid poplars was sent to us by Vogelsang (3) in 1942. All trees were thereupon cultivated twice in the spring of their second year's growth, without, however, any perceptible improvement in growth.

A conscientious effort was made to make the soil site and cultural practices conform with those observed at Midland, Michigan, the source of most of our trees, where there exists an excellent plantation of hybrid poplars. It is believed that this was achieved and the results are interpreted accordingly.

DISCUSSION

In a program of crop genetics, the poor results described could be expected and interpreted on an ecological basis. Thus the best hybrid corn strains in Wisconsin frequently, if not usually, fall considerably below their level of productivity in the nearby state of Michigan. Trees undoubtedly have a greater degree of climatic adaptation and tolerance than corn, but it is too often assumed that such factors as hardiness and drouth resistance are the chief limiting factors to successful growth in the case of forest trees. The generalization that "Broad-leaved trees easily adapt themselves to a warmer climate by prolonging their whole course of development" (1) is doubtless generally true and can be supported by considerable evidence, but it is equally obvious that climate alone does not include all the factors involved in the ecological optima of trees. That

trees like poplars will fail to respond to the more benignant climate and longer growing season of North Carolina and instead seem to prefer the climatic rigors of Michigan or New England may seem physiologically anomalous and contrary to their own best interests, but we believe it is so and must accept it. The obvious corollary would seem to be for the South or any other region to cease depending entirely upon demonstrably superior growing species or hybrids from other sections of the country, and to start selection and breeding with the best species at hand. Not that plant introduction and the trial of new species should not be included in a forest genetics program, but that perhaps less dependence should be placed upon this aspect.

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ADDITIONS TO THE FLORA OF SOUTH CAROLINA

By Budd E. Smith

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For ten years work has been done in making a thorough study of the flora of Darlington County in the coastal plain of South Carolina. This investigation has revealed several plants which are new to the flora of the state. All literature known to me dealing with its flora has been checked, and it is felt that the species listed below are now noted for South Carolina for the first time. Herbarium specimens have been placed in the herbaria of The University of North Carolina and of Coker College.

The most important early works covering this region, wholly or in part, are Thomas Walter's *Flora Caroliniana* (1788) and Stephen Elliott's *Sketch of the Botany of South Carolina and Georgia* (1821–24). Later came Ravenel's *Native and Naturalized Plants of South Carolina* (1883). Dr. W. C. Coker published his *Plant Life of Hartsville, S. C.*, in 1912. Dr. S. A. Ives of Furman University has published check-lists for Horry and Greenville counties, and Dr. Kenneth Hunt of The College of Charleston added in 1943 some plants to the recorded flora of the coastal plain. Various other papers have come out from time to time (see bibliography).

In 1931 when this work was begun the author was closely associated with Dr. J. B. Norton, who had worked with the Plant Introduction Commission of the United States Government. He had studied the plants around Hartsville for several years and gave great assistance in this study.

The following species with brief notes are offered as additions to the flora of South Carolina.

Amaranthaceae

Froelichia floridana (Nutt) Moq.

Rare plant of sandy fields near Lynche's River. Range extended north from Florida.

Caryophyllaceae

Stellaria fontinalis (Short and Peter) Robinson

Rare introduction found in lawn of Coker College. Range extended east from Tennessee and Kentucky.

Stellaria graminea L.

An introduced weed of lawns. Range extended south from Virginia. Small does not mention this plant in his flora of the southeastern states.

Rosaceae

Amelanchier arborea (Michx.) Fernald

Found along the west banks of Lauther's Lake. Range extended south from North Carolina.

Crataegus maloides Sarg.

Along streams on Witherspoon Island. Frequent. Range extended north from Florida.

Rubus nigrobaccus Bailey
Rich soil near Sonoco Products Plant at Hartsville. Southern limit extended to include South Carolina.
Rubus Baileyanus Britton
. Open hillsides throughout the area. Range extended south from North Carolina.

Leguminosae

Cracca Rugelii (Shuttlw.) Heller
Rare plant of dry pinelands. Range extended from southern Florida.
Rhynchosia mollissima (Ell.) S. Wats.
Dry pinelands. Rare. Range extended north from southern Georgia.
Galactia brevipes Small
Woolly prostrate plant of pinelands north of Hartsville. Range extended north from Georgia.
Lespedeza texana Britton
Sandy soil on Witherspoon Island. Rare. Range extended from Mississippi and Texas.

Oxalidaceae

Oxalis Priceae (Small) n. comb.
An introduced weed found in lawns in Hartsville. Range extended to include the southern coastal plain for first time. Only reported from Alabama and Kentucky.
Oxalis Langloisii (Small) n. comb.
Damp woods along west side of Lauther's Lake. Range extended north from Florida.
Oxalis macrantha Trelease
Open woods near Lauther's Lake east of Darlington. Range extended north from Florida and southern Georgia.

Polygalaceae

Polygala Harperi Small
Damp soil on Witherspoon Island. Rare. Range extended north from Florida, Louisiana, and southern Georgia.

Euphorbiaceae

Ditaxis humilis (Engelm. and Gray) Pax.
Dry sandy soil on Witherspoon Island. Rare. Range extended east from Kansas, Louisiana, and Texas.
Tragia linearifolia Ell.
Frequent in sandy soil and dry pinelands around Hartsville. Range extended north from Florida and southern Georgia.
Euphorbia Blodgettii Engelm.
Common on pure white sand dunes on Witherspoon Island. Range extended from southern Florida.
Euphorbia conferta (Small) n. comb.
Frequent in sandy soil on Witherspoon Island. Range extended from southern Florida.
Euphorbia hirsuta Torr.
A frequent weed in low moist places in Coker College Garden. Range extended south from Virginia.
Euphorbia humistrata Engelm.
An introduced weed of lawns in Hartsville. Range extended from Tennessee to coastal South Carolina.
Euphorbia zinniiflora (Small) n. comb.
Sandhills north of Hartsville. Range extended north from Florida.

Euphorbia exserta (Small) n. comb.
Sandhills north of Hartsville. Reported from this area by Dr. W. C. Coker in 1912, but has never been included in Small's Flora.

Vitaceae

Vitis rufotomentosa Small
Sandy hillsides on Witherspoon Island. Range extended from Florida.

Malvaceae

Sida carpinifolia L. f.
Weed of gardens and fields in vicinity of Hartsville. Range extended north from Florida.

Hypericaceae

Hypericum glomeratum Small
This plant has never before been reported from the coastal plain. Its only habitat has been the mountains of North Carolina. Several plants were found along a stream bed near Darlington. Range extended south to include coastal South Carolina.

Cistaceae

Lechea prismatica Small
Sandy woods on Witherspoon Island. Rare. Range extended north from Florida.

Melastomaceae

Rhexia Nashii Small
Damp soil on Witherspoon Island. Rare. Range extended north from Florida.

Onagraceae

Isnardia spathulata (T. & G.) Small
Wet soil along edges of ponds on Witherspoon Island. Range extended north from Florida.

Ericaceae

Vaccinium liparium (Small) n. comb.
Damp woods along the east side of Kilgore's branch north of Hartsville. Range extended south from North Carolina.

Vaccinium holophyllum (Small) n. comb.
Woods along west slope of Lauther's Lake. Rare. Range extended north from Florida.

Primulaceae

Lysimachia producta (A. Gray) Fernald
Damp soil along railroad west of Hartsville. Rare. Range extended south to South Carolina.

Apocynaceae

Apocynum medium Greene
Sandy soil along east side of Kilgore's branch east of Hartsville. Very rare. Range extended south from North Carolina.

Convolvulaceae

Ipomoea barbigera Sims
Waste area near Coker's Seed Warehouses at Hartsville. Range extended north from Georgia.

Boraginaceae

Myosotis arvensis (L.) Willd.
Low moist meadow on north side of Prestwood Lake at Hartsville. Range extended south from North Carolina.

Labiatae

Scutellaria Altamaha Small
Dry woods along the Timmonsville highway south of Hartsville. Rare. Range extended north from Georgia.

Lamium purpureum L.
Fields and gardens on farm of A. H. Rogers near Society Hill. Range extended south from North Carolina.

Heliotropiaceae

Cochranea anchusaefolia (Poir.) Guerke
Moist soil along roadside north of Darlington. Rare. Range extended north from Georgia.

Solanaceae

Lycopersicon cerasiforme Dunal
Waste places throughout the vicinity of Hartsville. Range extended north from Florida.

Solanum sisymbriifolium Lam.
Frequent in rich soil in McKinnon woods west of Hartsville. Range extended north from Florida.

Physalis nyctaginea Dunal
Dry pinelands north of Hartsville. Rare.

Scrophulariaceae

Ilysanthes grandiflora (Nutt.) Benth.
Low moist places in lower part of Kalmia Gardens west of Hartsville. Range extended north from Florida.

Acanthaceae

Ruellia humilis Nutt.
Sandy soil in McKinnon Woods west of Hartsville. Rare. Range extended north from Georgia.

Ruellia hybrida Pursh.
Edges of pinelands and thickets in vicinity of Hartsville. Range extended north from Florida.

Rubiaceae

Diodia rigida Cham. and Schlecht.
Sandy soil on Witherspoon Island. Range extended north from Florida.

Cucurbitaceae

Melothria crassifolia Small
Rich woods along west side of Lauther's Lake. Very Rare. Range extended north from Florida.

Campanulaceae

Specularia leptocarpa (Nutt.) A. Gray

Moist soil in meadow on farm of Roy Gandy near Dovesville. Very rare. Not previously reported east of the Mississippi River.

Compositae

Gnaphalium uliginosum L.

Frequent in rich soil of waste areas around Hartsville. Range extended east from Tennessee.

Gnaphalium spathulatum Lam.

Waste places and ditches along roadsides. Range extended north from Florida.

Vernonia recurva Gleason

Dry pinelands near Hartsville. Range extended from southeastern Georgia.

Eupatorium jucundum Greene

Woods near Darlington Country Club. Range extended north from Florida.

Laciniaria Garberi (A. Gray) Ktze.

Sandy soil near Hartsville Golf Course. Range extended north from Florida.

Tagetes minuta L.

A common weed in waste areas around Hartsville. Range extended south from North Carolina.

Chrysopsis Nuttallii Britton

Sandy pinelands west of Hartsville. Range extended from North Carolina.

Pityopsis oligantha (Chapm.) Small

Moist pinewoods west of Hartsville. Range extended from Alabama.

Solidago plumosa Small

Sandy soil along Kilgore's Branch east of Hartsville. Rare. Range extended south from North Carolina.

Solidago gracillima T. & G.

Damp pinelands near Kellytown west of Hartsville. Range extended north from Georgia.

Mulgodium villosum (Jacq.) Small

Roadside near Society Hill. Rare. Range extended from Florida.

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TWO SPECIES OF SEPTOBASIDIUM FROM MEXICO WITH UNUSUAL INSECT HOUSES*

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Plates 15 and 16 and Four Text Figures

The various species of fungi now included in the genus *Septobasidium* are closely related taxonomically to the rusts and live in conjoint symbiosis with scale insects on the stem and leaves of various seed plants. In this partnership the fungus furnishes a home and protection for the scale insects, while from the insects the fungus gets its food and a means of distribution.

During the winter of 1940 the writer spent some time looking for these fungi in Mexico, making in all over five hundred collections many of which were of undescribed species. Studies on several of these species brought to light additional information on the symbiotic relationships between these fungi and scale insects, and in this paper two of the species which show exceptionally interesting adaptations between fungi and insects are to be described.

The first of these two was found on *Fraxinus Uhdei* at Zitacuaro and Uruapan, causing marked damage to the host tree. As a rule the region of infection enlarges until it becomes several times as thick as the normal diameter of the limb (text-fig. 1). Numerous *Fraxinus* trees were seen at Zitacuaro and Uruapan on which many of the limbs were heavily infected and many other limbs were dead. One of the large public squares at Uruapan was surrounded by *Fraxinus* trees every one of which was heavily infected by this fungus.

Septobasidium fraxini n. sp.

Resupinate, forming circular patches up to 12 cm. in diameter on the branches of *Fraxinus*, frequently causing swellings, constrictions or witches' brooms. Tough and firm in texture; light buff or pinkish buff in the marginal region (5–10 mm. wide), shading rather abruptly to a dark cinnamon brown or rarely nearly blackish brown in the older part. Surface of new growth characteristically marked by numerous elliptic or crescent-shaped openings which lead into tunnels and chambers in the context; openings 40–160 x 200–370 μ, usually abundant, varying from 50 to 130 per sq. cm. of marginal region, disappearing or becoming much less conspicuous in the older parts, the surface of which is usually divided by numerous, irregular cracks into areas 1–3 mm. square. Margin abruptly determinate, smooth or minutely serrate. In section 0.8–1.5 mm. thick, composed of (1) subiculum, (2) context, (3) hymenium. Subiculum of compacted, hyaline or pale brownish hyphae. Context 0.6–1.3 mm. thick, composed of compactly entangled, hyaline or pale brown, sparingly branched, thick-walled hyphae, 3.8–5.4 μ thick, extending upward from the subiculum. Hymenium

* The collecting trip to Mexico was made possible by a grant from the Carnegie Corporation of New York.

arising from the context, 60–90 μ thick, deep brown in lower half, hyaline in upper part, formed of closely packed, upright hyphae and probasidia; hyphae thick-walled, brownish, 4.5–6.3 μ thick, the ends thin-walled, hyaline, 4.2 μ thick, and extending horizontally along the surface of the hymenium; probasidia hyaline, thin-walled, club-shaped, long-pyriform or sometimes nearly cylindrical, 9.6–12 x 16.8–26 μ; germinating and becoming empty to form a straight, typically 4-celled basidium 5.4–7 x 42–65 μ, which is frequently attached to the

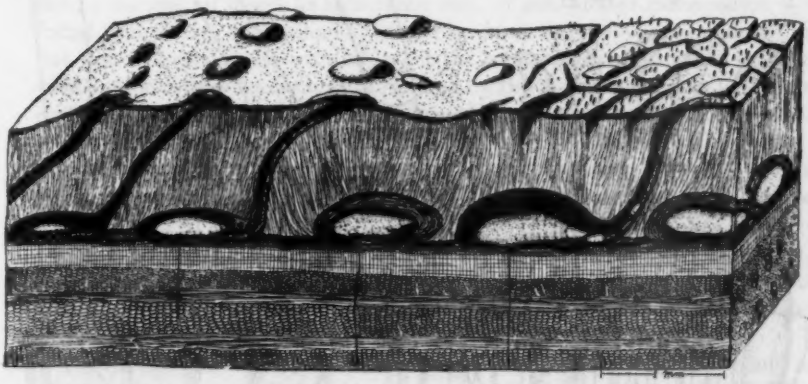
TEXT FIG. 1. Photograph of part of a *Fraxinus* tree in Morrow yard, Zitacuaro, Mexico, showing swollen limbs caused by *Septobasidium fraxini*.

probasidium by a short stalk and always projects entirely beyond the hymenial surface; sterigmata stubby. Mature spores not seen.

Associated with scale insects, some of which are parasitized by irregularly coiled haustoria of the glomerulus type, while others are free from parasitism. Distinguished by its occurrence on *Fraxinus*, the rounded symmetrical patches, the buff-colored margin, the elliptic or crescent-shaped openings to the insect houses in the younger parts and the finely-cracked surface of the older part.

The fungus-insect relationship in this species presents one of the most striking examples of mutual adaptation for symbiosis yet found in the genus *Septobasidium* (text-fig. 2). The insect houses here are formed before the young hatch and are located in the marginal region of the fungus. The newest houses are in

a row near the edge and the older ones in rows which become more irregular as development proceeds (Pl. 15, fig. 2). When the new houses are first recognizable they are shaped like shallow bath tubs with the slanting end directed toward the older part of the fungus. The floor of the tub is the subiculum and the sides and ends are vertical hyphae arising from it (Pl. 15, fig. 2, below). The hyphae grow from the side and front walls of these tub-like structures, arching over the floor to form a roof up to one millimeter thick. However, the roof is incomplete at the slanting end so that a minute tunnel with a floor like a toboggan

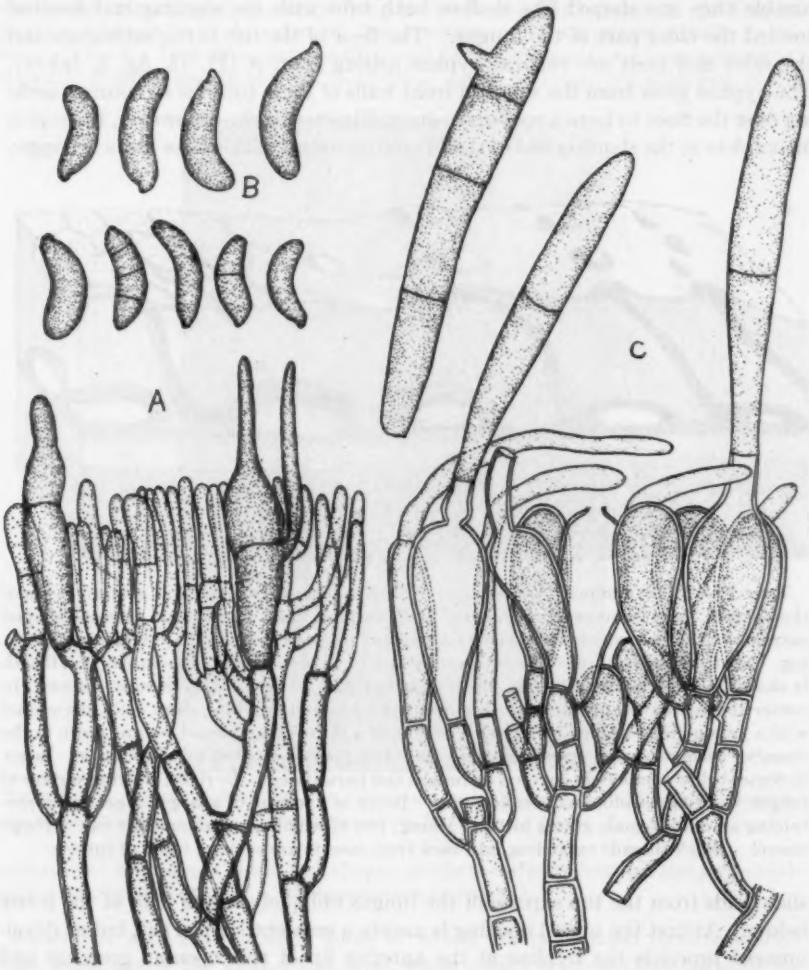


TEXT FIG. 2. Diagrammatic drawing of *S. frazini*, showing surface and section views of the fungus, insect houses, and insects. Top surface (left) shows four crescent-shaped entrances tc houses, with section view of a fifth and part of a tunnel with young insect entering. Next are shown three older entrances which have become igloo-like in shape; a fourth is shown in section with a young insect that has just settled in the chamber below. In center above are two entrances, the top one partly blocked by white, waxy coils, the second with a young insect headed for it, and a section of a third with a tunnel leading down to the chamber occupied by an insect; entrance and tunnel partly blocked by white coils. Insect in center below completely covered by fungus and parasitized. To right, fruiting surface of fungus, showing basidia and basidiospores. Below is a section of a large fungal house containing an adult female giving birth to young, two of which are making their exit through tunnel. Black threads extending into bark from insects are sucking tubes of insects.

slide leads from the top surface of the fungus obliquely to the floor of the house below. At first the tunnel opening is merely a crescent-shaped slit, but as development proceeds the hyphae of the anterior lip of this opening grow up and backwards, forming a structure shaped like an igloo whose opening is always directed toward the older part of the fungus. Frequently one may find a house with two or more exits and not rarely several houses connected by openings through the side walls.

As a rule there is a distinct break in color between the new region of growth with the new houses and the older parts. Furthermore the surface of the older parts is usually broken by numerous minute cracks. The adult females giving birth to young are found in old houses beneath this cracked surface. The young

emerge through old tunnels or cracks, and, after crawling about over the surface, an insect may enter one of the "igloos," descend through the tunnel, and settle



TEXT FIG. 3. A and B, *S. soleare*. A, hymenium showing two 2-celled basidia, one with sterigmata. B, spores. × 960. C, *S. fraxini*, hymenium with probasidia and basidia. × 1045.

down in the chamber. The openings to the tunnels are just the right size and shape (60–170 μ high by 250–375 μ wide) to permit the thin-bodied young scale insects to enter (30–40 μ thick, 172 μ wide by 285 μ long) but are not large enough to allow the entry of thick-bodied mites that are sometimes abundant on the

surface of the fungus. Most of the houses have an occupant. Of the 143 examined 84 were inhabited, while 59 were empty. A few houses contained two insects but as a rule such houses were double. Though a single house is too small for more than one adult, it would be large enough for many young. Why, therefore, is only one insect, almost always, found in a single house? A large number of houses were examined to discover the reason. There was the possibility that after an insect entered, the opening might close by rapid growth of the hyphae in this region. And, indeed, a few houses were found with doors partly or entirely closed by hyphal growth, but such houses were just as likely not to contain an insect as to contain one. Upon further examination it was found that houses with tunnels blocked by fungal tissue were exceedingly rare, but that in every house with an insect the tunnel leading into that house contained loose coils of waxy threads excreted by the insect. Three or four loops of such coils actually extended up into the entrance to the tunnel. Such structures could and may offer a mechanical barrier to the entry of a second insect, or the coils may serve merely to inform the insect that the house is already occupied. These waxy threads, to be effective in preventing the entry of a second insect, must be formed immediately after the insect enters the chamber. Although the waxy, coiled threads undoubtedly serve as an effective barrier to insects of the same or of different species which might want to enter the openings, it is questionable if such barriers are necessary, for in the species described below where no such barriers are formed only one insect ever settles in a house.

The fungus was collected in March before the end of the dry season and none of the young examined showed any signs of infection. It is very likely that infection occurs here as in *S. Burtii*, by the bud cells from the basidiospores. In the region of new growth no infected insects were found, but in the old tissue there were vast numbers of infected adults.

Specimens examined:

Mexico: Michoacan, Zitacuaro, by dirt road south of town, on *Fraxinus*, March 7, 1940, J. N. Couch and James Hinton, colls., Nos. 11498, 11499; on *Fraxinus* trees in Morrow yard, Nos. 11506, 11507, 11511, 11515; also on same trees, Mrs. Morrow, coll., April 20, 1940, Nos. 12778 and 12779. (Also seen on *Fraxinus* trees on the main square at Uruapan but none collected.)

The second of the two species to be described here was collected from a small deciduous tree about one half mile northwest of the village of Tamazunchale. The sandal-shaped insect houses in this species are perhaps the most remarkable in the entire genus. From their shape the fungus receives its name.

Septobasidium soleare n. sp.

Resupinate, forming distinct patches up to 8 cm. long, often girdling the smaller branches. Surface light cinnamon drab to cinnamon drab (Ridg.) when dry, deep brownish drab when moist; broken by numerous, irregular cracks formed by a splitting of the tissue, or by holes left in the incompletely formed top layer; also roughened by minute bumps or by spines which are nothing more

than pillars projecting through the top layer. Margin determinate. In section 1–1.5 mm. thick, composed of three distinct regions: (1) the subiculum, (2) the middle region of pillars, and (3) the top layer. Subiculum thin, near light cinnamon drab in the marginal region, which is characterized by the occurrence of one or more rows of closely spaced, sandal-shaped pens, the walls of each of which are formed by a thin plate of hyphal tissue. Just behind these are one to several rows of pens which are covered over except for a small area in the rear. Pens 0.5–0.8 x 1.2–1.6 mm. From the subiculum at the margin of each pen arises a palisade of black bristles or pillars which extend upward about 1 mm. and then branch out horizontally to form the beginning of the top layer. The top layer over each pen is at first V- or U-shaped or circular if viewed from above, but as the edges of the top layer meet a horizontal sheet of tissue is formed which is broken by cracks and holes, as mentioned above. Top layer 84–126 μ thick, composed of hyphae 2.8–4.2 μ (most about 3.8 μ) thick, the hyaline ends of which extend vertically to form the hymenium. Hymenium 40–60 μ thick; basidia arising directly from the hyphae without the intervention of a probasidial cell, 5.8–6.5 x 25–30 μ, club-shaped, 2-celled by a median transverse septum, one

TEXT FIG. 4. Diagrammatic drawing of marginal region of *S. soleare*. On left are four new insect houses; next a row of four houses with side walls and first roof. The roof is turned back in two houses to show that insect settles in end of house opposite opening. The next two rows of houses show colonnade of pillars and second roof. First roof of house in foreground partly removed to show adult insect giving birth to young. Note young insect crawling over fungus.

sterigma about 2.8 x 20 μ arising from each cell. Spores bent-elliptic, 4–6.3 x 14–24 μ, most about 5 x 16 μ, becoming once to thrice septate.

Associated with scale insects (Phenacaspis ? sp.), some of which are parasitized by haustoria in the form of irregular coils, which are connected with the subiculum through the vaginal pore.

Easily recognized by the shoe-shaped young insect houses on the margin, the irregular top surface frequently broken into U- or O-shaped parts, and by the cinnamon drab color.

In text fig. 4 a part of the marginal region, magnified about 16 times, shows diagrammatically the development and structure of the insect houses and the behavior of the young insects. The houses and insects are also shown photographically on plate 16. The new insect houses are formed in the marginal region, and back of them to the center of the fungus are rows of older houses. One or two new rows of houses appear to be formed each rainy season. Each

house starts as a roughly elliptic line of upward-extending hyphae forming an enclosure open at the posterior end, i.e., away from the margin. The tips of the hyphae grow inward to meet in a mid-line running lengthwise and thus forming the roof of the house except in the posterior part which is left open (Pl. 16, fig. 4, and text fig. 4). Meanwhile a closely set row of pillars grows up around the edge of the insect house. These extend upward about 1 mm. or slightly more and then branch horizontally from their tips to form a second roof. The mature house is shaped like a mummy case, with an opening at the smaller end (text fig. 4, right).

The insect houses formed in this species are the most efficient yet seen in the genus. These houses seem to afford ample protection against the scale insects' worst enemies, the parasitic hymenopterous wasps, as well as against the weather. The development of the wasp is as follows. A female wasp lays an egg in a scale insect. This egg develops at the expense of the scale insect, using up its entire body contents and eventually metamorphosing through larval and pupal stages to the adult which chews its way out through the old body of the scale insect and through the fungal covering, leaving a round and characteristic hole in the surface of the fungus. Careful search has been made in this species for these holes but not one has been found. Apparently the closely set colonnade of pillars and the top layer effectively prevent the wasps from reaching the scale insects and depositing their eggs.

Another striking thing about the houses is the relation between the number formed and their occupancy by insects. There appears to be neither a housing shortage nor an over-production of them. The roofs were removed from fifty-one of the completed houses: three were empty, while forty-eight contained insects in various stages of development. In none of the houses was there more than one insect. This is true although each house is large enough for several dozen young scale insects. However, the adult pregnant female almost completely fills the house, thus making it impossible for two adults to occupy the same house. Several times I have observed a young insect crawl into a house and then out immediately, presumably because it found the house already occupied. I have also tried transferring the young crawling insects to new houses. If the house were unoccupied, the insect might settle down in it, but if occupied by another scale insect, young or adult, the newcomer invariably crawled out to search for another house. Instinct here amounts to foresight, for something seems to tell the young insect that only one should settle in a house.

Another fact indicating the close coordination between the insects and fungus is that the young insects always settle in the *houses*, never in the alleys between them or elsewhere on the surface of the fungus.

When the fungus was moistened, spores were formed abundantly over the surface and since the scale insects were still hatching, it seemed of interest to try to determine how infection occurred. Young insects crawling over the damp sporulating top surface were lifted off with a needle under the binocular microscope and examined in water on slides under a high-powered microscope. Although many spores were found on the bodies of the insects, no signs of infection

could be found. It is thought that the original penetration occurs through the vaginal pore. After the females have moulted the last time, one can find a column of hyphae extending into the vaginal pore (Pl. 16, fig. 3). In some of the younger insects the hyphae near the vaginal pore are dark and thick-walled, while those farther up the vagina are hyaline. From the upper part of this penetrating column of hyphae branches extend out through the wall of the vagina into the haemocoel and there form irregular coils. In insects just infected, only a few coils have been formed, while in those which have been infected for some time the posterior part of the body is rather well filled with coiled haustoria.

The column of hyphae in the vaginal pore connects with the hyphae of the subiculum, this being the only connection which the fungus has with its host. The parasitized insects live several times as long as the uninfected insects, sucking the juices of the host tree. The fungus, in turn, through its haustoria, robs the parasitized insects of a large part of this nutriment, which is transported out through the column of hyphae and the subiculum to the peripheral, growing region to furnish material for the building of more fungal houses. In spite of the fact that certain of the insects are restricted in their normal life activities, in that they cannot reproduce, the fungus-insect relationship, in all species of *Septobasidium*, may be considered one of conjunctive symbiosis, where the symbionts are so intimately blended as to form an apparently single organism.

Specimens examined:

Mexico, San Luis Potosi, Tamazunchale, on deciduous tree, March 18, 1940, J. N. Couch, coll. (U. N. C. Herb. No. 11517).

EXPLANATION OF PLATES

PLATE 15

Septobasidium frazini n. sp.

Fig. 1. Showing enlargements (galls) caused by fungus and insects. Zitacuaro, Mexico. No. 11511. Nat. size.

Fig. 2. Openings to insect houses and depressions on lower margin which become houses. Same locality as above. No. 11498. × 7.

Fig. 3. Showing "roof" of house removed and insect inside. No. 11498. × 22.

PLATE 16

Septobasidium soleare n. sp.

Fig. 1. Showing surface and margin. Nat. size.

Fig. 2. Insect houses; note early stages of formation (above). × 7.

Fig. 3. Adult infected insect, fungal connection through vaginal pore (V). × 150.

Fig. 4. Insect house with insect inside. × 22.

Fig. 5. Same a few minutes later with insect outside house after its discovery that the house was occupied. × 22.

PLATE 15

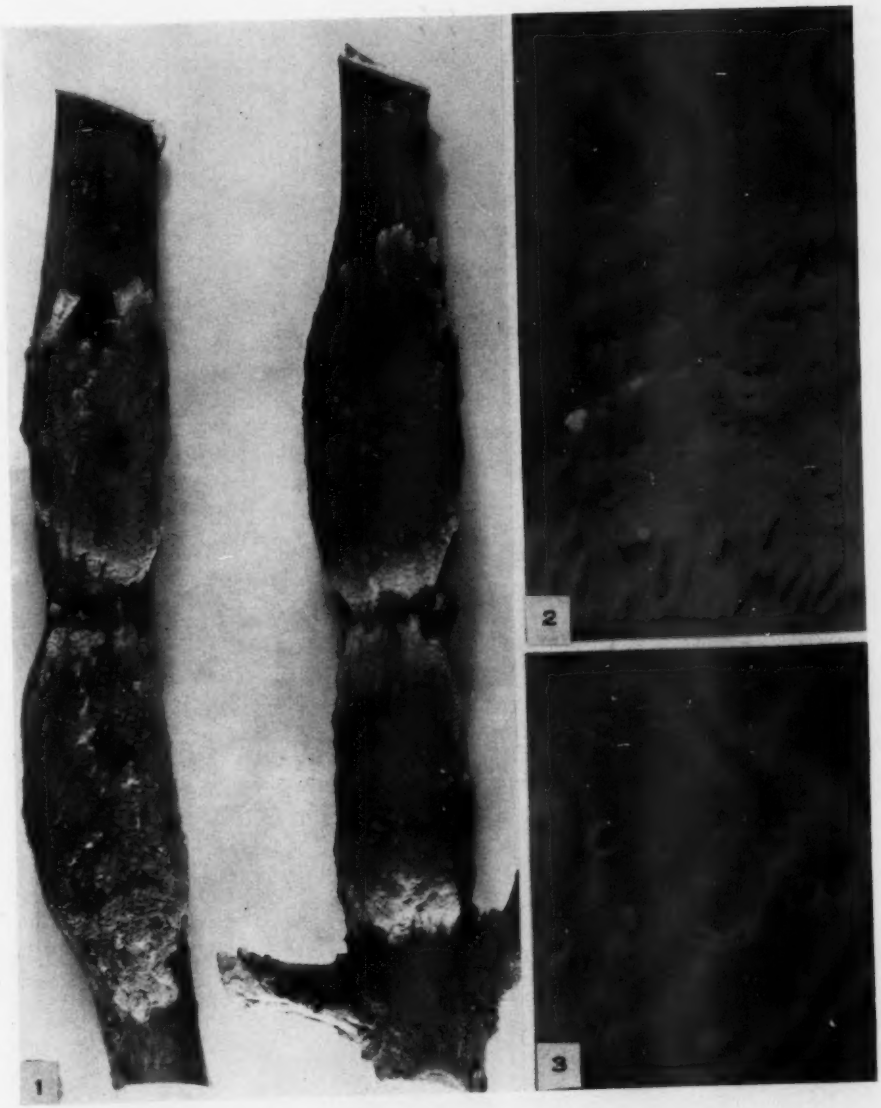
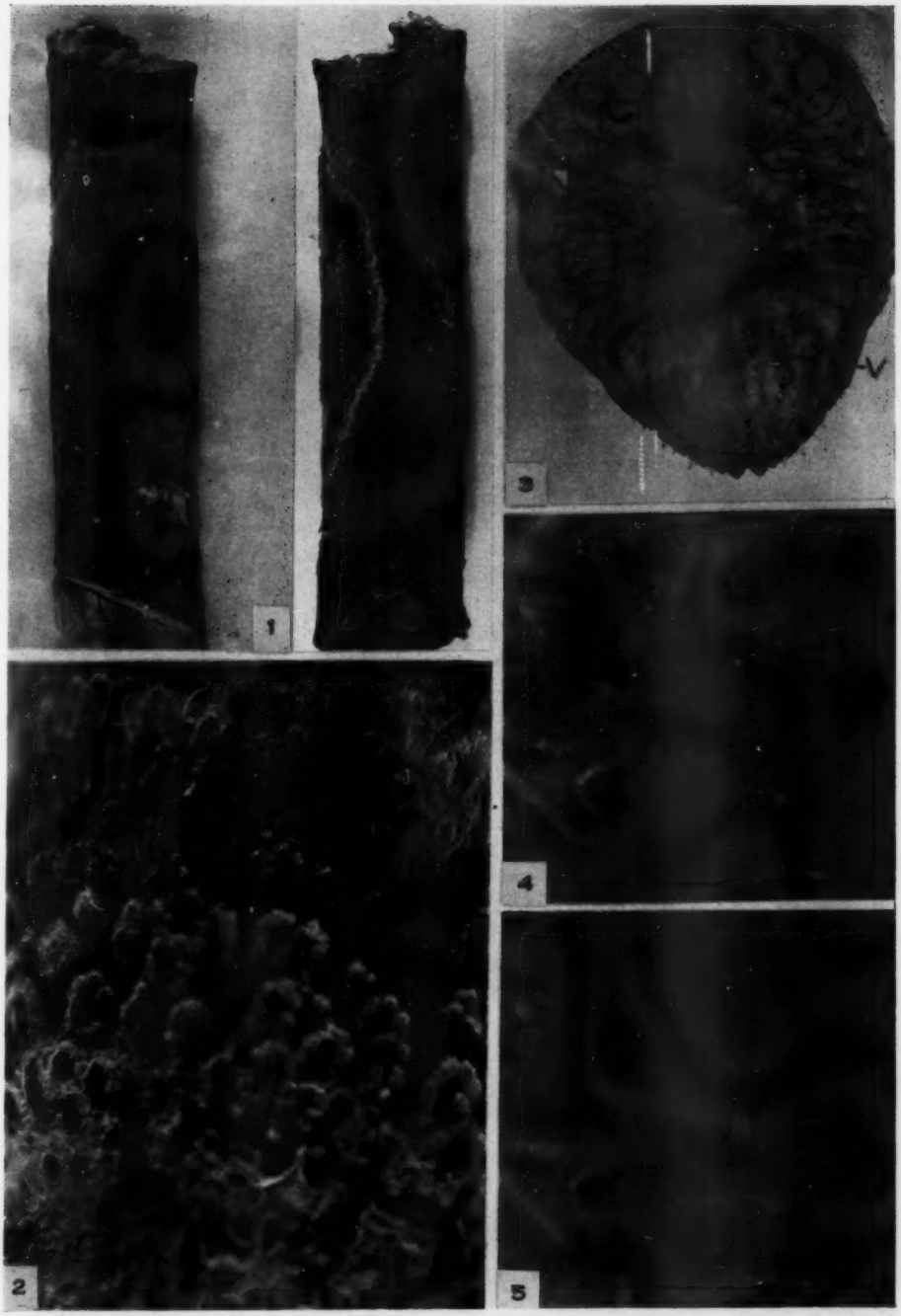


PLATE 16



THE UNITED STATES SPECIES OF COLTRICIA

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Plates 17–22

Without any intention of trying to improve on the various proposed subdivisions into genera of the old cohort of species known as *Polyporus*, a task that must be left to those with more experience in this field, I would like to record here the results of my studies of *Coltricia*, as treated by Murrill in North American Flora (**9**: 91–94. 1908).

Of the seven species (one tropical) included in the genus by him, five of the United States species seem to me a very natural group; the other, *C. tomentosa* (in which he includes *P. circinatus* Fr.), with its conspicuous setae, duplex flesh, and white spores, seems out of place. *Coltricia Memmingeri* Murrill I have treated before as a good species (Journ. E. M. Sci. Soc. **55**: 381. 1939) from what seemed at the time sufficient evidence. Since then I have come to the conclusion that it really is an excessively stout form of *C. obesa* (= *C. Montagnei*), "a very obese *obesus*," as Lloyd put it. Murrill has since added to the genus a new species from Florida, *C. Mowryana*, which I note but have not collected.

For the study of this group one could find no better place than Highlands, N. C., where I have had an opportunity to study them for a good many summers. Two of them (*Montagnei* and *cinnamomea*) are so common there that they can be found on any walk along mountain roads in July and August, and a third (*perennis*) is not at all uncommon in white pine woods. As *C. Montagnei* seems rare or little known in the north, I have given most space to its consideration.

The group of five species here treated as *Coltricia*, together with the little polypore treated by Murrill as *Coltriciella*, may be characterized as follows:

Annual on earth or humus or duff or (in Nos. 5 and 6) on rotting wood; some shade of brown throughout (grayish in age in *focicola*), stalked, flesh very thin (except in forms of *Montagnei*); tubes usually short, the mouths at first thickened with a fine whitish or brownish fluff or felt, becoming concolorous; spores brown, ovoid or elliptic, smooth; setae lacking.

In the following key are included two plants with conspicuous setae and white spores, treated by Murrill under *Coltricia* that we here include under *Polyporus*.

Setae lacking; flesh homogeneous; spores brown (*Coltricia* and *Coltriciella*)
  Growing on the ground and in humus or duff
    Cap zonate, flesh very thin; stem slender
      Surface strongly lustrous; spores 4–5 x 5–7.5 μ ..... (1) *C. cinnamomea*
      Surface dull or subshining
        Tubes very variable, usually rather large (0.5–2 mm.); spores 3.7–5(6) x 6.7–10 μ; growing on burnt-over ground ..... (2) *C. focicola*
        Tubes small (0.5 mm. or less); spores 3.7–5.2 x 7–8.5 μ; growing in coniferous woods (3) *C. perennis*

Cap not zonate or obscurely so, flesh thicker; stem slender to stout; spores 6–7(7.5) x 11–12(13) μ ..... (4) *C. Montagnei*
Growing on rotting wood of Red Bay (Florida) ..... (5) *C. Mowryana*
Growing pendent from dead wood, otherwise much like *C. cinnamomea*; spores 4–5.5 x 6–8.5 μ ..... (6) *Coltriciella dependens*
Setae conspicuous; flesh duplex; spores white; growing under or on conifers
Setae straight or nearly so ..... (7) *Polyporus tomentosus*
Setae strongly curved ..... (8) *P. tomentosus* var. *circinatus*

(1) **Coltricia cinnamomea** (Jacq.) Murrill. N. Amer. Flora **9:** 91. 1908.
Boletus cinnamomeus Jacq. Coll. **1:** 116. 1786.
Polyporus splendens Peck. Bull. Buf. Soc. Nat. Sci. **1:** 61. 1873.
Polyporus subsericeus Peck. Rept. N. Y. St. Mus. **33:** 37. 1880.
(This is a renaming of *P. splendens*.)
Polystictus cinnamomeus (Jacq.) Sacc. Michelia **1:** 362. 1878.

Plate 18, figs. 1–3; pl. 22, figs. 1, 2

Cap usually about 1.5–2 cm. wide, very rarely 4 cm., depressed to umbilicate in center, surface rich chestnut brown, with the texture and luster of satin or a moth's wing and very delicately radially lined with inherent fibers which later may become loosened, especially in the center, thus making it finely hispid; margin at first even, then beautifully fimbriated or in age lacerated. Flesh very thin, hardly ¼ mm., firm but pliable even when dry.

Tubes angular, very short, about 1 mm. or less, rather large for so small a plant, 1–2 mm. wide, the walls thin with uneven or frayed edges, covered at first inside and out with a delicate whitish or buffy brown felt which disappears gradually, leaving the pores colored like the cap or darker in age.

Stem central, about 2 or 3 cm. long and 2–3 mm. thick, velvety, usually enlarged below into a little mat or pad, just as in *obesa*, only on a minute scale.

Spores light cinnamon color, oblong-elliptic, with a large oil drop, smooth, 3.8–5.5 x 6–8 μ (average of 14 collections 4.3–5.1 x 6.5–7.6 μ).

This exquisite little plant is common in the mountains and not rare in the piedmont and coastal plain on bare or mossy banks of roads and streams. It grows in deciduous woods and prefers a firm footing on soil, unlike *perennis* showing no affinity for conifers. Among our rather numerous collections (33) and the many seen and not taken, in only one case was it growing in any connection with conifers and that was on very rotten pine wood. It may be noted that several species of fungi that are not associated with conifers have been grown to full maturity on a medium containing ground pine wood (Etter, Mycologia **21:** 197. 1929). Unlike *focicola*, *cinnamomea* has no liking for burnt-over ground or ashes. Rarely it is found on much decayed wood (presumably hardwood).

The plants are usually circular but may be irregular or lobed, occurring separately in small colonies or even singly, but at times they may be crowded with considerable fusion taking place both of the cap and bases, rarely the stems also (No. 12512). We have collected in Florida (No. 10329) a colony of about 25 plants all of small to very small size and growing from a mat of moss and fern on a palmetto trunk several feet from the ground. In appearance and spores it was exactly like the typical, differing only in consistently small size and peculiar

habitat. Some of them were growing directly from the tips of the moss and from their bases fine fibers could be traced down among the moss leaves.

Coltricia cinnamomea is distinguished from *C. focicola* by shorter tubes, smoother, more silky and more uniformly colored cap, smaller spores and no affinity for burnt-over soil; from *C. perennis* by smaller size, more silky-shining and regular cap, larger tubes, and growth in deciduous woods (but see No. 4537). *Coltricia perennis* is more lobed and often lacerated and tends to become more buffy and even grayish in age.

Illustrations: Atkinson. Stud. Amer. Fungi, fig. 182. 1900 (fig. 187 of 1901 ed.).
Bambeke. Bull. Roy. Soc. Bot. de Belgique **46:** pl. 1, figs. 1–7. 1909.
Hard. Mushrooms, fig. 344. 1908.
Jacquin. Collect. **1:** pl. 2. 1786.
Lloyd. Myc. Notes, Polyp. Issue No. 1, fig. 200 (as *Polystictus*). 1908.
Shope. Ann. Mo. Bot. Garden **18:** pl. 24, fig. 3. 1931.
Note: Bresadola's illustrations (Icon. Myc. **20:** pl. 953) do not look like our plant.

North Carolina. Chapel Hill. No. 323. In Battle Park, Oct. 2, 1911. No. 711. Mossy ground, June 20, 1913. No. 915. In sandy soil among lichens, Oct. 15, 1913. Spores 4.5–5.5 x 6–7.5 μ. No. 2163. In mixed woods south of campus, June 20, 1916. Spores 4–4.5 x 6.2–7.4 μ. No. 3348. In woods, June 12, 1919. No. 4520. July 10, 1920. Spores 4.1–4.8 x 6.8–7.6 μ. No. 4537. On *very rotten* pine wood, July 26, 1920.
Highlands. No. 10955. On road banks, Aug. 19, 1938. No. 11017. On bank in deciduous woods, Aug. 30, 1938. No. 11727. Same place as above, July 19, 1940. Spores (print) 4.2 x 6.6–7.5 μ. No. 11728. On bank in deciduous woods, July 19, 1940. Spores 4.8–5.5 x 6–7.5 μ. No. 12021. Road bank, non-coniferous woods, July 15, 1939. Spores 4.5–5.5 x 6.3–7.5 μ. No. 12063. July 30, 1940. Spores 4.5–5.5 x 7–8.3 μ. No. 12512. Mixed woods, Aug. 6, 1941. Stems much fused and branched. Spores 4.6–5.5 x 6.3–7.5(8) μ. No. 12539. Road bank, broad-leaved woods, Aug. 10, 1941. Spores 3.8–5.5 x 7–8.2 μ. Also many other collections from Highlands.
Standing Indian Mountain, Macon County. No. 10961. Bank by trail, Aug. 20, 1938. Spores 4–5.5 x 7.4–8.1 μ.
Pisgah Forest. No. 10995. On roadside bank, Aug. 23, 1938. Spores 4.4–5.5 x 7–8 μ.
South Carolina. Oconee County. No. 11809. At the junction of Whitewater and Thompson rivers, Aug. 3, 1940. Spores 5–5.8 x 7.6–8.4 μ.
Florida. No. 10329. On mossy trunk of Sabal palmetto with the fern *Phlebodium aureum*, 40 miles south of St. Augustine, Dec. 29, 1936. Colony of about 25 pigmy plants 5–10 (12) mm. broad. Spores 4.5–5.2 x 6–8 μ.
New York. Ithaca. July 4, 1906 (Coker).

(2) **Coltricia focicola** (B. & C.) Murr. N. Amer. Flora **9:** 92. 1908.
Polyporus focicola B. & C. Journ. Linn. Soc. **10:** 305. 1868.
Polyporus simillimus Peck. N. Y. St. Mus. Rept. **32:** 34. 1879.

Plate 17 and pl. 22, figs. 3, 4

Cap 1.2–4 cm. broad, regular or with margin more or less lobed, thin, deeply depressed to umbilicate in center, tomentose, multizonate and with more or less distinct rough radiating ridges; margin very thin, often minutely fimbriated in our plants; color a rusty cinnamon when fresh, the center lighter with a grayish drab over-color, soon becoming paler and in age buffy gray and appearing as if powdered. Flesh tough, semi-rigid and not so elastic as in *cinnamomea*, very thin, ¼–¾ mm. thick, a deep rust color, often appearing nearly black when cut in age.

Tubes up to 4 (rarely 5) mm. long near stem, shallower toward the margin, the

mouths variable in size both in different plants and in the same plant, sometimes less than ½ of a mm., again 2 mm. in diameter in the same colony; in youth both the mouths of the tubes and the broad sterile margin an ashy clay color from a soft felt, the inside of the tubes being darker, about Prout's brown (Ridg.), in age the whole underside of the plant becoming this color and the mouths strongly toothed or lacerated.

Stem central, even, 1–3 cm. long and 1.5–3 mm. thick, velvety, firm, tough, solid, colored inside and out like the darker parts of the cap.

Spores sordid brown, near Dresden brown, smooth, oblong, mucro minute, almost or quite invisible, very variable in size, 3.7–5 (6) x 6.7–9.5 (10) μ (average for eight collections 4.4–5.1 x 7.3–9.3 μ.

This species occurs in colonies, often numerous, and where crowded the caps frequently fuse. It is usually if not always confined to burnt-over woods or ash piles. While found as far north as New York, it is much more common in the southern states. Most of our collections have come from the coastal plain or piedmont. The addiction of the species to ashes has been noted by most authors, as Curtis (as *P. parvulus* Kl.), Overholts, Murrill, Lowe, and Lloyd (see also Murrill in Bull. Torr. Bot. Club **31:** 345, 1904, as *C. parvula;* and Peck, l.c., pp. 33 and 34, as *P. parvulus* and *P. simillimus*).

This plant as understood in America is supposed not to occur in Europe. Some European descriptions of *perennis*, as Rea's, might very well include this species also. He speaks of *perennis* as growing on charcoal heaps but in America *perennis* does not have this habit, while *focicola* does. See under *perennis* for suggested confusion of these two species in America.

Illustrations: Lloyd. Myc. Notes, Polyporoid Issue No. 1, fig. 203 and fig. 204 (right). 1908.

Shope. Ann. Mo. Bot. Garden **18:** pl. 26, fig. 3 (as *P. perennis*). 1931.

North Carolina. Chapel Hill. No. 1297. Growing in and near ashes, July 20, 1914. Spores 3.7–4.4 x 6.7–8.2 μ. No. 1380. Under pines in a burnt-over place, scattered over an area about 30 feet wide, Oct. 19, 1914. Spores 4.8–5.4 x 7–8.5 μ (print). No. 1404. In ashes in woods, Oct. 22, 1914. Typical, brown when young, gray in age, zones darker. Old specimens in this collection were colored green by an alga (*Pleurococcus*). No. 1555. In ashes, June 19, 1915. No. 1811. On a rocky hillside where trash had been burned a year before, Sept. 17, 1915. These plants were quite dry and the color was very light, buffy-gray or nearly white, broad zones separated by deep brownish-black ones, or all the zones light. Stem and tubes buff. Spores 4.2–4.8 x 8.5–9.7 μ. No. 1998. On an ash pile, Nov. 23, 1915. Gray and strongly zoned. No. 2376. Mixed woods, Battle Park, July 8, 1916. Spores 5.8–6.7 x 7.5–10 μ.

Highlands. No. 10955b. On bank by road, Aug. 19, 1938.

Blowing Rock. No. 5685. By roadside, Aug. 22, 1922.

Haywood Co. On burnt-over ground on Cold Spring Mountain, Aug. 3, 1926. Spores 4.3–5 x 6.8–8.5 μ. Tube mouths very small.

South Carolina. No. 30. In burnt-over place in pine woods, June 29, 1917. No. 5862. In mixed woods, Aug. 31, 1922. Spores 3.7–4.8 x 7.5–9.5 μ.

Tennessee. Montvale Springs. No. 3. Oct. 16, 1927 (L. R. Hesler, coll.). Also a collection on burnt-over soil, July 14, 1928 (Hesler; det. by Overholts). Color buffy gray; large pores; spores 4.5–4.8 x 8–10 μ.

Florida. Gainesville. On burnt soil, Aug. 20, 1926 (H. E. Bratley, coll.). Buffy gray in color; spores 4–4.8 x 7–10 μ. Another collection, July 25, 1931 (E. West).

(3) **Coltricia perennis** (L) Murrill. Journ. Mycol. **9**: 91. 1903.
Polyporus perennis Fr. Syst. Myc. **1**: 350. 1821.
Polystictus perennis (L.) Karst. Rev. Myc. **3**, No. 9: 18. 1881.
Polyporus connatus Schw. (according to Lloyd, Myc. Notes, Polyp. Issue No. 1: 8. 1908.
Coltricia connata Gray. Brit. Plants **1**: 644. 1821.

Plate 18, figs. 4–6; pl. 22, figs. 5, 6

Cap usually 2-5.5 cm. broad, rarely up to 8 cm., glossy or dull ochraceous tawny, darker and more reddish when dry, zonate; margin slightly convoluted and finely fringed, often with lobes and flaps. Flesh concolorous, 1 mm. or less thick, fibrous, elastic.

Tubes 0.8–2 mm. long, rarely 3 mm., tube surface even, mouths very small, 3 (4) to a mm., nearly circular, tubes covered at first with a whitish or pale buffy brown felt, then gradually darker until concolorous with cap at full maturity, the mouths becoming more or less toothed or torn in age.

Stem very variable, up to 4.2–5 (6) cm. long and 5–6 mm. thick, crooked, surface plush-like, *uneven* with nodules and short ridges, concolorous, base blunt, not enlarged or rooted.

Spores light brown, oval, 3.7–5.2 x 7–8.5 μ (average of 6 collections, 3.9–4.7 x 7–8 μ), mucro minute, almost or quite invisible. Basidia 4-spored, about 5–6 μ thick.

On soil or duff under conifers (pine, hemlock).

Shope's illustration looks more like *focicola* and his description seems to include both. He, Murrill, and Lowe say *perennis* likes burnt-over places, and Rea, in England, says it grows in "charcoal heaps and about stumps." Overholts in Washington University Studies located it "on burned-over earth in woods," but does not repeat this in his later work, The Polypores of Pennsylvania. In our experience *perennis* has no such habit, and we think that associating this species with fire is due to confusion with *focicola*. It is generally thought that *focicola* does not occur in Europe, but from Rea's statement above it looks as if both species may occur there and have been similarly confused. In our collections the cap of *focicola* is distinctly more regularly circular and more hoary in age, the spores and tubes average larger, and the growth is on burnt soil rather than on unburnt soil under pines. The variation in tube size in *focicola* is extreme, even in the same colony. (Note the two plants on right in bottom row of photograph of our No. 1380. In these two and in all of the Haywood County colony the tubes were 2–3 to a mm.). Lowe gives *Polyporus parvulus* var. *deformatus* as a synonym of *focicola*, but in my opinion it is *P. Montagnei*.

Etter (Mycologia **21**: 197. 1929) grew *perennis* to maturity with normal caps in a culture medium containing powdered pine wood. Fitzpatrick finds that it may be parasitized by *Claudopus subdepluens* Fitz. (Mycologia **7**: 37, pl. 153. 1915). The same small plant may also parasitize *Cantharellus cibarius* (Mycologia **21**: 279. 1929).

Illustrations: Hard. Mushrooms, pl. 47. 1908.
Krieger. Nat. Geog. Mag. **37**: pl. 7. 1920. Note that this shows growth from coniferous needles (hemlock).
Lloyd. Myc. Notes, Polyp. Issue No. 1, fig. 201.
Sowerby. Engl. Fungi, pl. 192. 1799.
Note: Bresadola's illustrations (Icon. Myc. **20**: pl. 959) look much more like *focicola*.

North Carolina. Chapel Hill. No. 4519. Mixed woods in flat above Meeting of the Waters, July 26, 1920. Typical; cap 5.7 cm. wide; spores 3.7–4 x 7–8 μ.
Highlands. No. 11737. Under pines by Ravenel Lake, July 20, 1940. No. 11757. In pine needles on Farnsworth place, July 23, 1940. No. 11776. In pine needles, July 28, 1940. No. 11854. In pine needles on Farnsworth place, Aug. 10, 1940. Spores 3.8–4.6 x 7.2–7.6 μ. No. 12120. In Anderson pine grove, Aug. 8, 1939. Spores 4.4 x 6.3–7.5 μ. No. 12335. Under white pines, Aug. 3, 1931. Spores 4.2–5.1 x 7.2–8.4 μ. No. 12464. On banks, July 28, 1941. Large plants up to 6 cm. broad but tubes hardly 0.8 mm. deep though shedding spores (good print). No. 12513. Under white pines and rhododendron, Aug. 6, 1941. Spores 4.2–5.2 x 7–8 μ. No. 12730. In Anderson pine grove, Aug. 30, 1941. No. 12738. Under pines on Sargent place, Sept. 2, 1941. No. 13003. At entrance to Sargent place, Aug. 18, 1942. Spores 3.7–4 x 7.4–8.5 (8.9) μ. No. 13491. Under hemlock and birch, Aug. 17, 1943.
Blowing Rock. No. 7519. Under white pines, Sept. 3, 1924.
Connecticut. Earle, coll. (U. N. C. Herb. from N. Y. Bot. Gard. Herb.) Spores 4.6 x 8 μ.

(4) **Coltricia Montagnei** (Fr.) Murrill. Mycologia **12**: 13. 1920.
Polyporus Montagnei Fr. *In* Montagne, Ann. Sci. Nat. II, **5**: 341, 1836; Epicr. Syst. Myc., p. 434, 1836–38.
Polyporus parvulus var. *deformatus* Peck. Rept. N. Y. St. Mus. **32**: 33–34. 1879.
Polystictus obesus Ell. & Ev. Bull. Torr. Bot. Club **24**: 125. 1897.
Coltricia obesa (Ell. & Ev.) Murrill. Bull. Torr. Bot. Club **31**: 346. 1904.
Coltricia Memmingeri Murrill. Bull. Torr. Bot. Club **31**: 347. 1904.
Polystictus cuticularis Lloyd. Myc. Notes, Polyporoid Issue No. 1: 12. 1908.

Plates 19, 20; pl. 22, figs. 7–11

Plant very variable; cap 1.7–9.5 cm. broad, delicate to massive, convex, plane or depressed, usually irregular and rugose, not zonate except at times for a few obscure growth zones, the center roughened with pits and ridges; surface soft and velvety or spongy-tomentose, rarely fibrous-scaly, color about cinnamon brown to deep russet brown, margin paler when growing, thick or thin, usually entire or rarely incised, not truly fimbriate, turning deep reddish brown when rubbed; flesh concolorous, not zonate, soft corky above, becoming firmer downward, 1-20 mm. thick, tough, pliable and fibrous, shining when dry, strongly bibulous; odor when dry distinctly aromatic, not unpleasant.

Tubes more or less decurrent, usually short, 1–4 mm. long, rarely 6 mm., very rarely in large plants up to 8 mm. near the stem, the mouths at maturity usually of unequal size, 1-2 mm. wide, often elongated near the stem, the margins uneven but not jagged, covered at first with a matted felt of pale threads which also cover the sterile underside of the cap margin, becoming dark red-brown when rubbed.

Stem very variable, slender or massive, usually about 1–4 cm. long, expanding below to a thick irregular rooting base or into a superficial pad or mat with no

sign of root, surface concolorous, velvety, texture hard and rigid, the basal thickening also firm except for the surface.

Spores rusty brown, ellipsoid, smooth, 4.5–6.5 (7.5) x 8–12.5 (13.5) μ (average of 21 collections 5.2–6.1 x 9.4–11.3 μ). Basidia large, variable, 2–7-spored, more commonly 4-spored, sterigmata large and usually spreading (see Journ. E. M. Sci. Soc. **55:** pl. 44, figs. 9–11. 1939).

Growing on the ground in broad-leaved (very rarely coniferous) woods and often on bare gravelly roadside banks in such woods, never in our experience attached to wood of any kind.

In the Blue Ridge Mountains of North Carolina this species is more common than any other of the group except perhaps *cinnamomea*. It is apparently much rarer in other parts of the country. It seems to have been reported from this country first by Berkeley in Lea's Catalogue of the Plants of Cincinnati (1849) as *Polyporus Montagnei*. The next report of it we find was by Peck as *P. parvulus* var. *deformatus* (l.c.). We have seen the type collection of this variety kindly sent us by Dr. House and find it a good expression of *Montagnei* in all respects; spores 5–6.7 x 9.5–11.2 μ. Overholts had determined it as *P. focicola* and Lowe gives it as a synonym of that species. Peck says it "sometimes occurs on shaded banks by roadsides." Next it is found in New Jersey and Pennsylvania and described by Ellis and Everhart as *Polystictus obesus*. Thanks to the kindness of Dr. Fred Seaver, we have received from the New York Botanical Garden the Ellis and Everhart collections marked type. There are two separate labels both from Newfield, N. J. The larger collection, consisting of four plants and supposedly the more authentic type, is marked "Ground in low woods, Sep. 6, 1897"; the other, consisting of two smaller immature fused plants is marked "Ground amongst leaves, Sept. '97." These are all probably from the same original colony. On the first label is written "This (sec Patouillard) is *Polystictus Montagnei* Fr." We find the spores of this lot to be about 6.3 x 11 μ, agreeing essentially with our measurements and with those given by Overholts and Lowe, not 4–5 x 7–8 μ, as given by Ellis and Everhart and by Murrill. There is also a box of two plants of *C. obesa* (and so labelled) in the New York Botanical Garden collected by Murrill and House in Pink Bed Valley, N. C., marked "Oak-chestnut woods and Kalmia-Rhododendron thickets, No. 537." The spores of this are also large, 5 x 10 μ. Other collections of this species in the same herbarium are: Hebron, N. H., Aug. 6–19, 1905, Percy Wilson, coll., as *obesa*, and Buck Hill Falls, Pa., Mrs. Delafield, coll., as *Montagnei*. The spores of this last are 5.5–6.5 x 9.5–11 μ. In none of the examples above mentioned is there any sign that they were associated with conifers and none is attached to wood. In the case of *Montagnei*, European authors make no mention of a coniferous habitat. It is now generally admitted that this is the same as *obesa*, although the spores of the former as given by European authors are too small (Rea, 4–5 x 5–6 μ; Bresadola, 4–6 x 7–9 μ).

Coltricia Montagnei has two distinct methods of attachment: (1) from a below-ground ball or irregular tuber which comes up densely covered with gravelly soil or humus, or (2) from a thin or rather thick mat that extends out flat on bare soil and is attached to it only by very delicate strands of the concolorous

mycelium. In plants with large pores and flesh not too thin a peculiar condition may be easily observed that we have not seen in any other polypore. A section will show that from the bottom of many of the pores very small more or less circular tunnels or extensions may run out at an angle a short distance into the cap. These tubules are lined with pale hymenium just like the larger tubes. This condition indicates that the cap flesh is homogeneous with the tube context and this is further indicated by the slightly uneven penetration of the tube bases into the cap flesh. These last two characters are those assigned to the genus *Trametes*, but the spores are brown and not white (see under *Coltriciella dependens*).

It will be seen from the synonyms above that we now consider *C. Memmingeri* only a very large and heavy *Montagnei*. Since the publication of our note in the Mitchell Journal (**55**: 381. 1939) we have found at Highlands, N. C., a number of forms connecting the massive plants with those of ordinary size, and one of ordinary size (No. 11825) was taken from the same spot as the massive No. 11011 illustrated in the article cited. The species is so common there that we have collected it 80 times and could have brought in many more. The extreme variability of this species is suggested by our illustrations. Including all these forms, the plant may be distinguished from all others, in the great majority of cases, by this combination of characters: rather large tubes, thicker flesh, thicker stem, swollen stem base, dull, azonate cap, and larger spores. While most of these characters may weaken at times, they never all fail in the same plant. The spores can always be relied on and the thick stem nearly always.

Illustrations: Bresadola. Icon. Myc. **20**: pl. 961, fig. 1. 1931.
Coker. Journ. E. M. Sci. Soc. **55**: pl. 40 and pl. 44, figs. 9–11 (as *C. Memmingeri*). 1939.
Lloyd. Myc. Notes, Polyporoid Issue No. 1: fig. 205 (as *Polystictus cuticularis*). 1908. This is an unusually zonate form. The name was changed to *P. Montagnei* in Letter 53, Notes 188, 195, and this change is correct, as shown by the type plants kindly sent us by Dr. J. A. Stevenson. The spores are 4.8–6 x 10–12 μ.
Quélet. Champ. du Jura et des Vosges, pl. 17, fig. 4.
Rea. Trans. Brit. Myc. Soc. **2**: pl. 11 (below). 1906.
Hussey. Ill. Brit. Myc., ser. 1, pl. 51 (as *P. perennis*). 1847.

North Carolina. Highlands. No. 10973. On roadside bank, Aug. 21, 1938. No. 11004. On roadside bank, Aug. 25, 1938. Spores 5.5–5.9 x 11–12 μ. Basidia 4-spored, about 9.4 μ thick; hymenium very pale, about 22–26 μ thick. No. 11011. In rhododendron woods near a spring, Aug. 30, 1938. No. 11706. On bank at Trillium Lodge, July 11, 1940. Spores 4.6–6.3 x 9.2–12.6 μ. No. 11712. Under white pines, July 13, 1940. No. 11714. On gravelly road bank, July 13, 1940. Spores 5.8–6.5 x 10–12 μ. No. 11825. In deep humus by a spring, Aug. 5, 1940. Spores 5.5–6.6 x 10–11.8 μ. No. 11890. Under broad-leaved trees in Primeval Forest, Aug. 18, 1940. No. 12000. On bare clay bank under mixed vegetation, July, 1939. Spores 5.5–7 x 9.8–11.5 (12.5) μ. No. 12007. On bank on Bear Pen Mt., July 11, 1939. Spores 6–6.7 x 10–12 μ. No. 12019. On a clay bank, hanging almost vertically under the bank, July 19, 1939. Spores 6.3–7.5 x 11–12.6 μ. No. 12020. On a clay bank, July 14, 1939. Spores 5.2–6.3 x 7.4–11.2 μ. Thin and delicate for the species. No. 12082. In humus in rhododendron woods near a spring, Aug. 4, 1939. No. 12229. On a gravelly bank, Aug. 25, 1939. Spores 5.5–6.5 x 8.8–11.4 μ. No. 12314. Same spot as No. 12082, Sept. 11, 1940. Spores 4.6–5.1 x 8.5–11.3 μ. No. 12484. Same spot as just above, Aug. 2, 1941. No. 12546. Same spot as above, Aug. 11, 1941.

Nos. 11011, 12082, 12314, 12484, 12546, all from the same spot, grew in a thick bed of humus and duff by a strong spring in dense mixed growth and were large heavy plants. The first two were treated by us as *C. Memmingeri* in Journ. E. M. Sci. Soc. **55**: 381, 1939. The spores as given there were too short. No. 11825, also from the same spot, was a much smaller plant, 4 x 5.5 cm.

Jackson County. No. 11719. On path from High Falls, July 16, 1940.

Blowing Rock. No. 5598. On bank under kalmia, etc., Aug. 19, 1922. Also reported by Atkinson and Schenck.

See text above for other plants examined.

(5) **Coltricia Mowryana** Murr. Bull. Torr. Bot. Club **67**: 228. 1940.

Plate 22, fig. 12

Dr. Murrill has sent us a fragment of this species and it is easily seen to be a very distinct plant, with very thin flesh, long tubes with minute mouths, shiny red-brown, multizonate cap, up to 10 cm. wide and rather stout stem. So far known only on rotting wood of *Persea Borbonia* in Florida, it is to be looked for farther north wherever the red bay grows. Our spore measurements from type are 4.2–5.5(6) x 7–8.5(9) μ, practically the same as given by Murrill. For a full description see Murrill, above cited.

(6) **Coltriciella dependens** (B. & C.) Murrill. Bull. Torr. Bot. Club **31**: 348. 1904.

Polyporus dependens B. & C. Ann. Nat. Hist. II, **12**: 431. 1853.

Polystictus dependens (B. & C.) Sacc. Syll. Fung. **6**: 213. 1888.

Trametes dependens (B. & C.) Baxter. Pap. Mich. Acad. Sci. Arts and Let. **14**: 267. 1931.

Plate 22, fig. 13

For the first time in Chapel Hill there has been found last fall by one of our students the rare and odd little plant here treated. It was originally collected on dead pine wood in South Carolina by Dr. M. A. Curtis, later on pine and oak in New Jersey (Murrill, l.c.), on *Liriodendron* in Florida (see Murrill, Southern Polypores, p. 42), from Long Island (Lloyd, Note 861), on chestnut in North Carolina (Baxter, l.c.), by Hesler on oak, Cades Cove, Tennessee (Rept. Reelfoot Biol. Sta. **5**: 1941), by Murrill on the bank of Newnan's Lake, Florida, and by Weber, West, and Murrill at Magnesia Springs, Florida, both the last two collections on standing stubs of red cedar and projecting horizontally with the tubes vertical. It has also been reported by Lloyd from Japan (Note 215) and from Africa (?) (Myc. Notes, Polyporoid Issue No. 1: 12. 1908).

It is a very small, stalked, snuff-brown plant, peculiar in its pendent habit, nearly always hanging from the under side of rotting wood. It has the general appearance of a dwarf *Coltricia* with the pores borne on the distal rather than the proximal side of the inverted cap. The sporophore is said to reach a width of 2 cm., but ours though fully mature are only up to 5 mm.

Baxter transfers the species to *Trametes*, but the spores are brown (rust colored), not hyaline as described for *Trametes* by most modern authors (Murrill, Overholts, Lowe, Shope, Bresadola). Baxter says "The position of the tubes

and their structure in relation to the context as shown by slides made from fixed material conclusively demonstrate that this plant should be placed in the genus *Trametes*." We suppose he means that the tube context is of the same kind of tissue as that of the adjacent cap layer and that the tubes are inserted at unequal depths. If brown-spored polypores with tough texture and pores as just noted are to be placed in *Trametes*, then *Coltricia obesa* must be placed there also and probably all other species here treated as *Coltricia*. For a discussion of the genus *Trametes* see Overholts, The Polyporaceae of Pennsylvania II (Pa. Agric. Expt. Sta. Bull. 316: 14. 1935) and Lowe, The Polyporaceae of New York State (Bull. N. Y. St. Coll. For. Tech. Pub. No. 60: 83. 1942).

The description of our collection follows.

A crowded group of pendent little plants springing from a spongy mass of dark cinnamon (about snuff brown or sayal brown, Ridg.) fibers; entire plant including the swollen spongy base up to 5 mm. long, the little stems strigose, expanding into the caps which in the smaller ones are shaped like a pestle or wine glass, in larger ones like a wasp's nest, as noted by Lloyd, the flat distal end circular or irregular, as 2 x 2 mm. or up to 2 x 5 mm.; pores about 0.5 mm. wide and 1 mm. deep, mouths thin and jagged. The entire plant is felted, silky-tomentose and concolorous with the basal pad. Even the pores before opening are covered with this silky felt, as they are also in species of *Coltricia*.

Spores (of No. 13630) brown, oval, smooth, 4–5.2 (5.5) x 6–8.5 μ. No cystidia.

In a letter to us (Nov. 2, 1945) Murrill sends us a note on the habit of the plants on cedar stumps mentioned above. After describing the normal form, Murrill writes as follows.

"On December 7, 1926, however, two abnormal collections were made in hammocks east of Gainesville, both on decayed stumps of southern red cedar. These will be described below.

"The first collection was made by myself on the west bank of Newnan's Lake; the second at Magnesia Springs by Weber, West and Murrill. The two agree in every particular. A few of the fruitbodies are normal, but most of them, growing as they did luxuriantly on the side of a moist, decayed, mossy stump, developed so as to *appear* conchate and sessile, not fitting the description of the species in either shape or size. Close examination, however, shows that practically all the hymenophores, even those reaching 2 cm. in width and much crowded, do have a short stipe attached to the vertex of the pileus, which would doubtless be pendent if it could."

Illustrations: Baxter. Pap. Mich. Acad. Sci. **14**: pl. 35. (1930) 1931.
Lloyd. Myc. Notes, Polyporoid Issue No. **1**: fig. 207. 1908.

North Carolina. Chapel Hill. No. 13630. Hanging from the under side of a rotting cedar pole at University Lake, Oct. 20, 1945. Roberta Lovelace, coll.

(7) **Polyporus tomentosus** Fr. Syst. Myc. **1**: 351. 1821.
Polystictus tomentosus (Fr.) Cooke. Grevillea **14**: 77. 1886.
Mucronoporus tomentosus Ell. & Ev. Journ. Myc. **5**: 28. 1889.
Coltricia tomentosa (Fr.) Murr. Bull. Torr. Bot. Club **31**: 346. 1904.

Plate 21; pl. 22, figs. 14–16

Plant very variable, 4–10 cm. broad, usually irregular and complicated by ridges and lobes, often zonate, convex to depressed, smooth with the texture of

kid or felted (subtomentose), warm buff (Ridg.) to darker reddish brown when fresh and somewhat water-soaked, much lighter, about antimony yellow or paler when dry, the margin almost white to orange, usually minutely jagged and very thin. Flesh thin, 1–7 mm. thick near center, deep brown (antique brown) to golden brown with tint of olive, duplex, firmly spongy above, much denser and more woody next the tubes, the two layers of equal or unequal thickness, firm and rigid and burning like punk when dry; no taste or odor. The surface imbibes water instantly.

Tubes small, 2 to 5 to a mm., sometimes widening by the breaking down of the walls, 2.5 mm. deep, color of flesh, the mouths grayish when young due to the extension of very delicate white threads, turning deeper brown with age and soon becoming jagged or toothed, not decurrent or only slightly so.

Stem central to excentric, usually short and thick but often longer and more slender, up to 7 cm. long when rooted; surface and color as in cap center.

Spores (of No. 12625) pure white when fresh (good print), not colored as supposed by Lloyd and Murrill, smooth, oval-elliptic, 3.2–3.8 x 5.5–7.2 μ. Hymenium containing numerous reddish, deeply seated, straight or rarely slightly irregular, sharp setae, 8–13 μ thick and projecting 25–50 μ, abruptly constricted at base.

Parasitic or saprophytic on pine, above or below the ground.

This species is evidently not closely related to the others put into *Coltricia* by Murrill. The conspicuous setae, the duplex flesh, and the white spores clearly indicate its lack of close relationship. *Polyporus tomentosus* Fr. and *Polyporus circinatus* Fr. are considered the same by Murrill. Our plants are exactly like the good plates of *tomentosus* given by Lloyd. Haddow (Trans. Brit. Myc. Soc. **25:** 179–189. 1941) has discussed at length the three proposed species, *tomentosus*, *circinatus*, and *dualis*, and comes to the conclusion that *circinatus* should be considered a variety of *tomentosus* distinguished only by its curved setae, and that *dualis* is identical with the latter. This seems to us a reasonable solution. That *dualis* was a form of *circinatus* was suggested by Ellis and Everhart in 1889 (l.c.). Lowe (Bull. N. Y. St. Coll. For., Tech. Pub. No. **60,** 1942) considers *dualis* of specific rank, but so far as our plants are concerned, the differences he gives do not hold, except for the curved setae. For example, spores of a plant from Cold Spring Harbor, Long Island (N. Y. Bot. Gard. Herb., as *C. tomentosa*), which has large and strongly curved setae, are 3.3 x 4.5–4.8 μ, and a plant from Sweden also with strongly curved setae has spores almost exactly the same; one from Massachusetts (Farlow Herb. No. 352, as *P. tomentosus*) has straight setae and spores 3–4 x 5.5–6.3 μ. Lloyd describes as *Polyporus peakensis* a plant from Pike's Peak, Colorado, which is probably this species. He finds setae but does not say whether straight or curved (Myc. Notes No. 62: 933. 1920).

Illustrations: Bresadola. Icon. Myc. **20:** pl. 960. Duplex flesh not shown.
Ellis and Everhart. Journ. Mycol. **5:** pl. 8 (as *Mucronoporus*). 1889.
Haddow. Trans. Brit. Myc. Soc. **25:** pl. 6, fig. 1. 1941.
Lloyd. Myc. Notes, Polyporoid Issue No. 1: fig. 197 (as *Polystictus*). 1908.
Shope. Ann. Mo. Bot. Gard. **18:** pl. 26, figs. 1, 2 (as *Polyporus circinatus*). 1931.

North Carolina. Highlands. No. 11984. Near foot of a large white pine, Sargent yard, Sept. 3, 1940. No. 12625. Same spot as just above, Aug. 19, 1941. No. 13578. Same spot as above, Sept. 6, 1943. Also Nos. 12315, 127 29 from Highlands.

Jackson County. No. 10938. In soil by roadside in open mixed woods, Whiteside Cove, Aug. 17, 1938. Spores 3.7–4.2 x 5–6.7 μ. Deep red, pointed, straight setae plentiful. No. 12996. Attached to the bark at foot of a white pine, near Cashiers, Aug. 18, 1942. Spores pure white, 3.7–4 x 5.1–7 μ. Strong red-brown setae as usual.

(8) **Polyporus tomentosus** var. **circinatus** (Fr.) Haddow. Trans. Brit. Myc. Soc. **25:** 187. 1941.

P. circinatus Fr. Monog. Hymen. Suec. **2:** 208. 1863. (See Haddow, p. 180.)

P. dualis Peck. Rept. N. Y. St. Mus. **30:** 44. 1878.

P. circinatus var. *dualis* Peck. Rept. N. Y. St. Mus. **49:** 30. 1896.

Plate 22, figs. 17, 18

Among our own collections we have only one (Georgetown, S. C.) that has setae that are of the *circinatus* type. It is attached by a very short central plug. Cap. 7.5 cm. wide, surface unevenly pitted, covered, where not worn off, by a very thin membrane which is buffy brown and minutely felted-pubescent. In this specimen the membrane has disappeared in large part except on the margin, leaving the darker rusty brown, spongy-fibrous context exposed. This is soft and punky, about 1.5 cm. thick near center and thick throughout except for the abruptly thin margin. It is composed almost entirely of the soft material but there is an extremely thin (less than 1 mm.), hard layer above the tubes that is visible in about half the cap. Tubes as in *tomentosus*, the marginal ones pale.

Spores white, 3.5–4 x 6–7.3 μ. Setae plentiful, dark red-brown, strongly curved, 11–14.8 μ thick and projecting about 40 μ.

Near Georgetown, S. C., on pine bark, Dec. 28, 1926.

The very thick flesh composed almost entirely of soft tissue led us to doubt the identity of this plant with *dualis*, but Overholts has determined it as such and kindly sent us a more typical example from State College, Pa., on dead *Pinus rigida*. This also has the hard layer very much thinner than the soft (about 1–2 mm. as compared to 10 mm. more or less). Peck's description of *dualis* will have to be modified to include subsequent collections. He says the two layers are about equal in thickness (repeated by Lowe) and the total thickness about equal to that of the pores. We are adopting the name proposed by Haddow. Note that Ellis and Everhart found the "hooked spines" in *dualis* (not mentioned by Peck) and suggest that it is probably a form of *circinatus* (Journ. Myc. **5:** 28. 1889).

This Georgetown specimen is the only one we have found. Lowe reports it rare, even in the home state of *dualis*.

Illustrations: Fries. Icon. Select., pl. 180, fig. 1.
Haddow. Trans. Brit. Myc. Soc. **25:** pl. 6, figs. 2, 3. 1941.
Lloyd. Myc. Notes, Polyp. Issue No. 1, fig. 198 and fig. 199 (as *Polystictus dualis*). 1908.

EXPLANATION OF PLATES

PLATE 17

Coltricia focicola. No. 1380. Nat. size.

PLATE 18

Figs. 1–3. Coltricia cinnamomea. 1, No. 12021 (dry state), nat. size; 2, No. 10961 (moistened after drying), nat. size; 3, one of same collection enlarged slightly. Note fimbriate edge.

Figs. 4–6. C. perennis. 4, No. 11854, long-stemmed form; 5, No. 12513; 6, No. 12335. All nat. size.

PLATE 19

Coltricia Montagnei

Fig. 1, No. 12693, young plant developing from conical mound of tissue. Fig. 2, No. 11004. Fig. 3, No. 10973, showing irregular, tuber-like base. Fig. 4, No. 12007. Fig. 5, No. 12000. Fig. 6, No. 11714, delicate plant. Fig. 7, No. 11842, tube surface showing irregular mouths. Fig. 8, No. 11706. Fig. 9, No. 12019, unusual form with cap rolled upward exposing the tubes. All nat. size.

PLATE 20

Coltricia Montagnei

Fig. 1, No. 12020, a thin and delicate form of this species. Bit showing tube surface somewhat enlarged. Fig. 2, No. 12044, nat. size. Fig. 3, No. 11842, nat. size. Fig. 4, No. 11712, a large, heavy form, slightly reduced. Fig. 5, No. 12082, slightly reduced.

PLATE 21

Coltricia tomentosa

(Above) No. 12996, × about ¾. (Below) No. 11984, nearly natural size.

PLATE 22

Fig. 1. Coltricia cinnamomea. No. 12539. × ¾.
Fig. 2. C. cinnamomea. No. 12539. Spores. × 1620.
Fig. 3. C. focicola. No. 1380. Small section of hymenium with one basidium. × 1012.
Fig. 4. C. focicola. No. 1380. Spores. × 1620.
Fig. 5. C. perennis. No. 4519. Small section of hymenium with one basidium. × 1012.
Fig. 6. C. perennis. No. 13003. Spores. × 1620.
Fig. 7. C. Montagnei. No. 12000. Bit of branched hypha. × 502.
Fig. 8. C. Montagnei. No. 11706. Basidium with 7 spores. × 810.
Fig. 9. C. Montagnei. No. 11890. Basidia with 2 spores each. × 810.
Fig. 10. C. Montagnei. No. 12229. Spores. × 1620.
Fig. 11. C. parvulus var. deformatus. Spores of type. × 1620.
Fig. 12. C. Mowryana. Spores of type. × 1620.
Fig. 13. Coltriciella dependens. No. 13630. Spores. × 1620.
Fig. 14. Polyporus tomentosus. No. 12315. Bit of hymenium showing straight setae. × 148.
Fig. 15. P. tomentosus. No. 10938. Two setae. × 502.
Fig. 16. P. tomentosus. No. 12625. Spores. × 1620.
Fig. 17. P. tomentosus var. circinatus. Georgetown, South Carolina. Spores. × 1620.
Fig. 18. P. tomentosus var. circinatus. Georgetown, S. C. Bit of hymenium showing curved setae. × 502.

PLATE 17

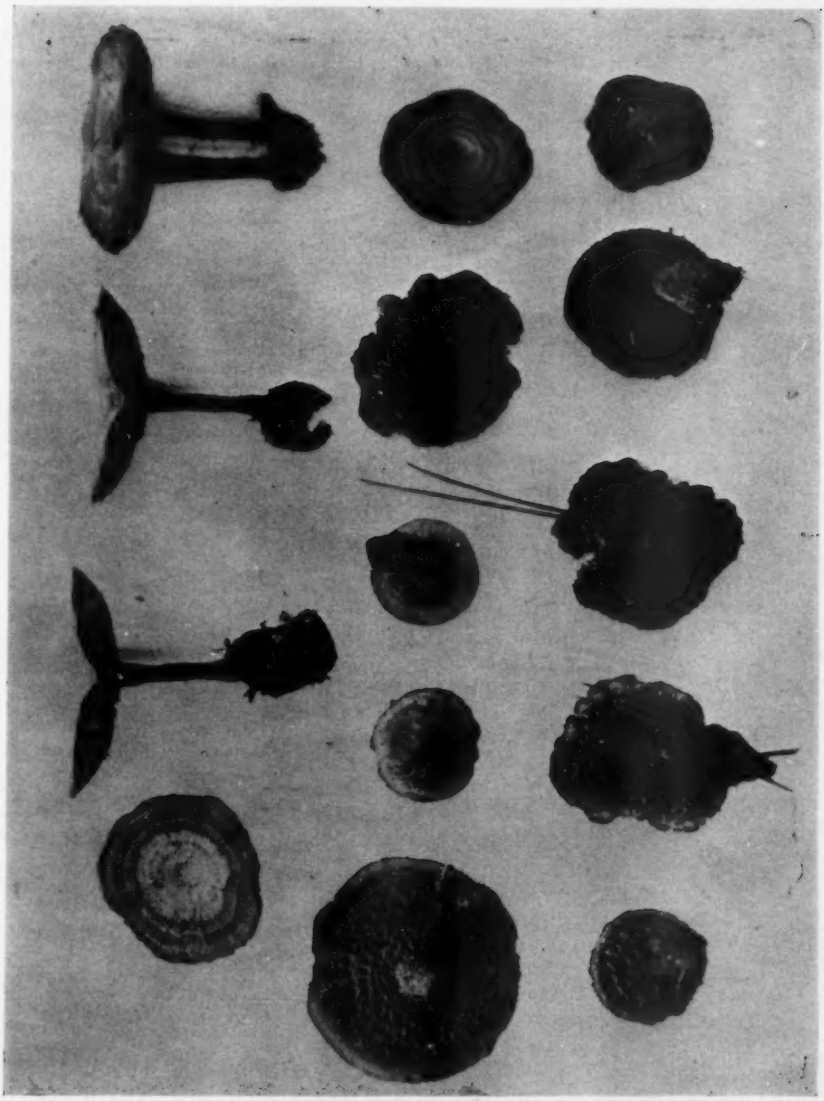


PLATE 18

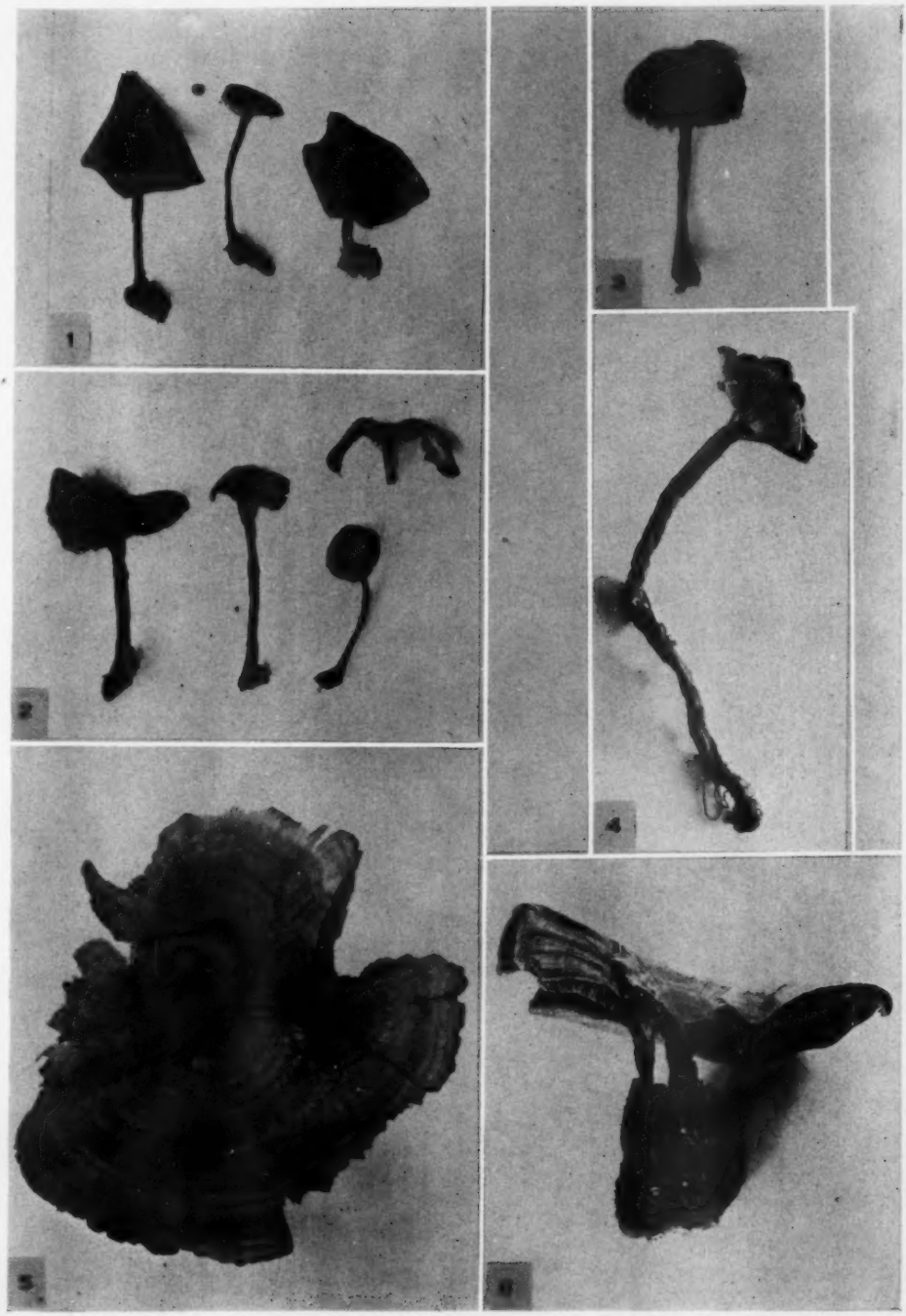
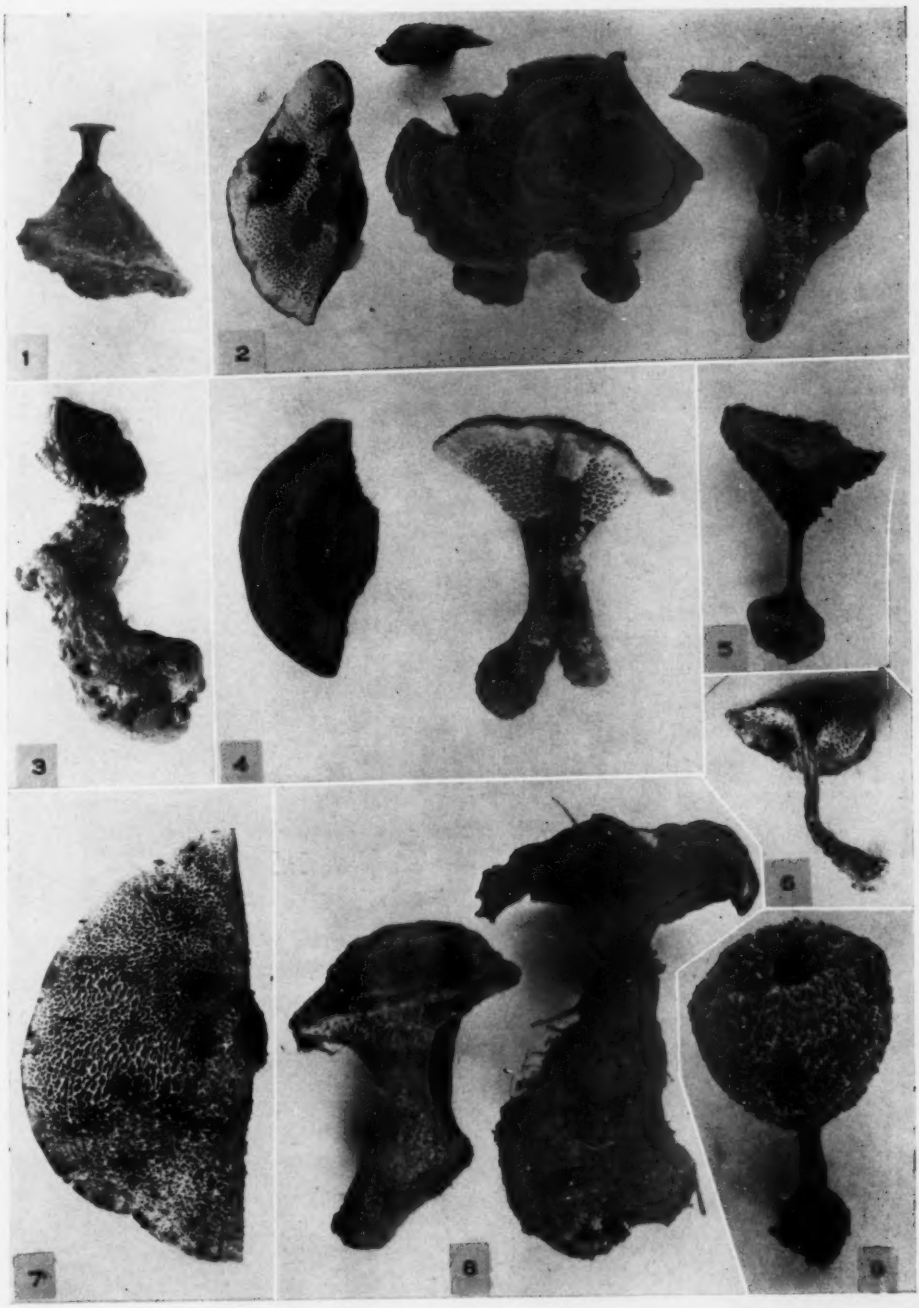


PLATE 19



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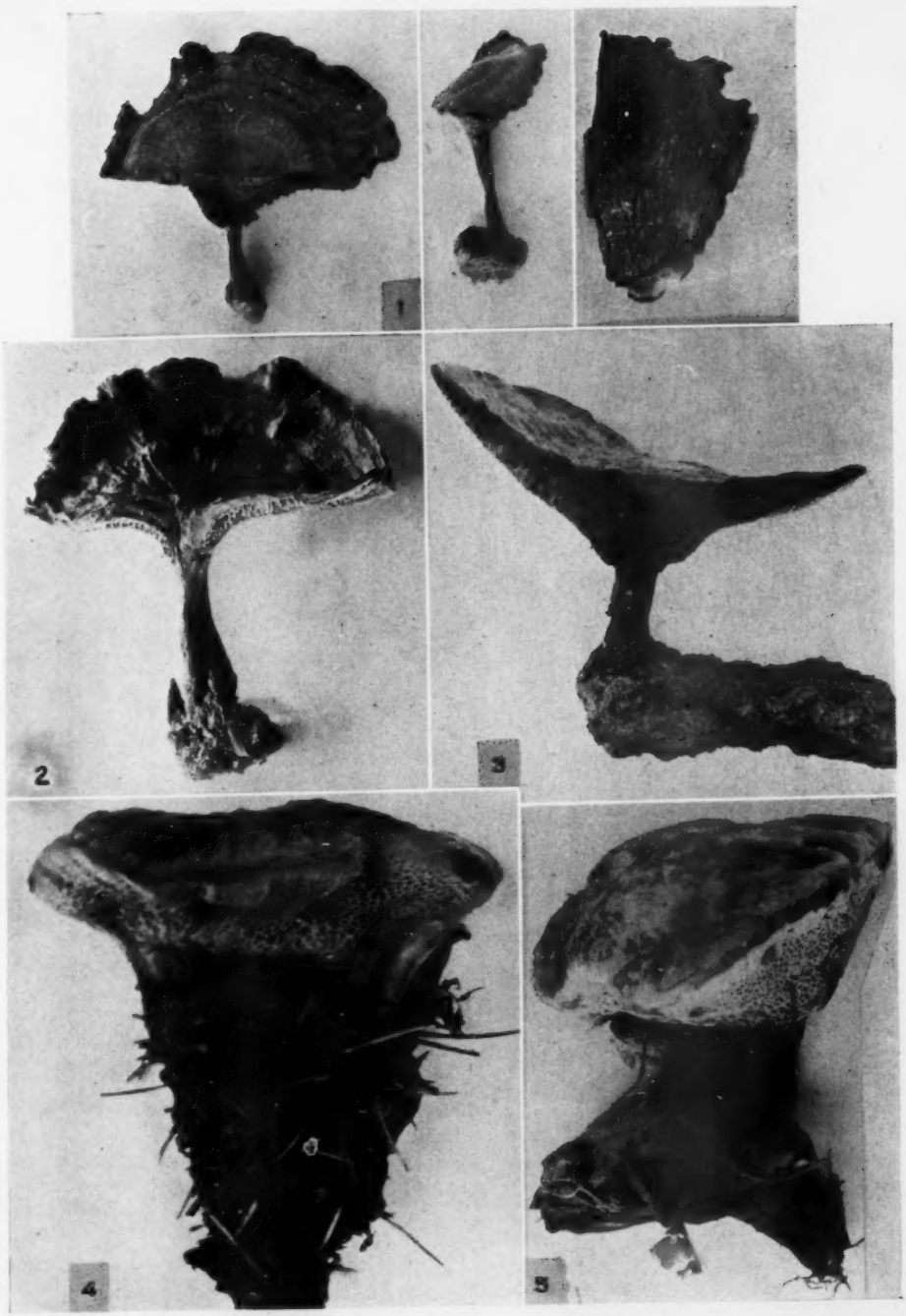

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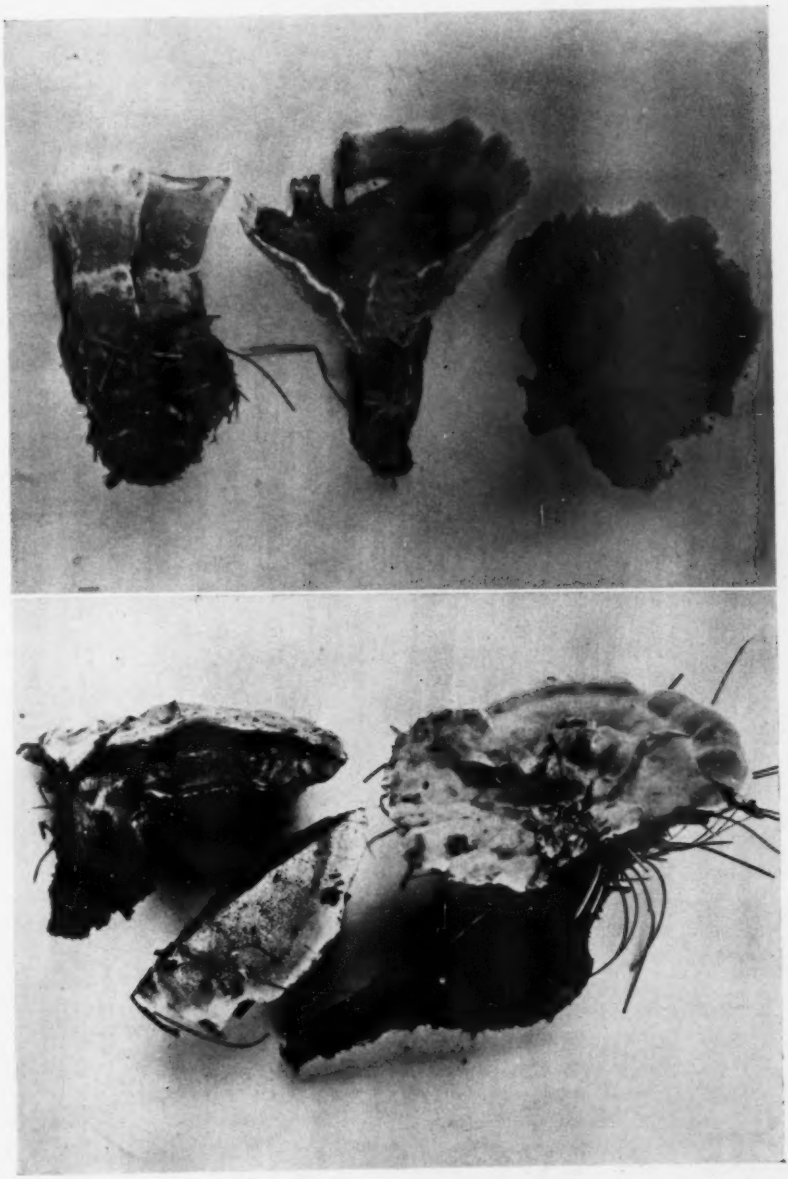
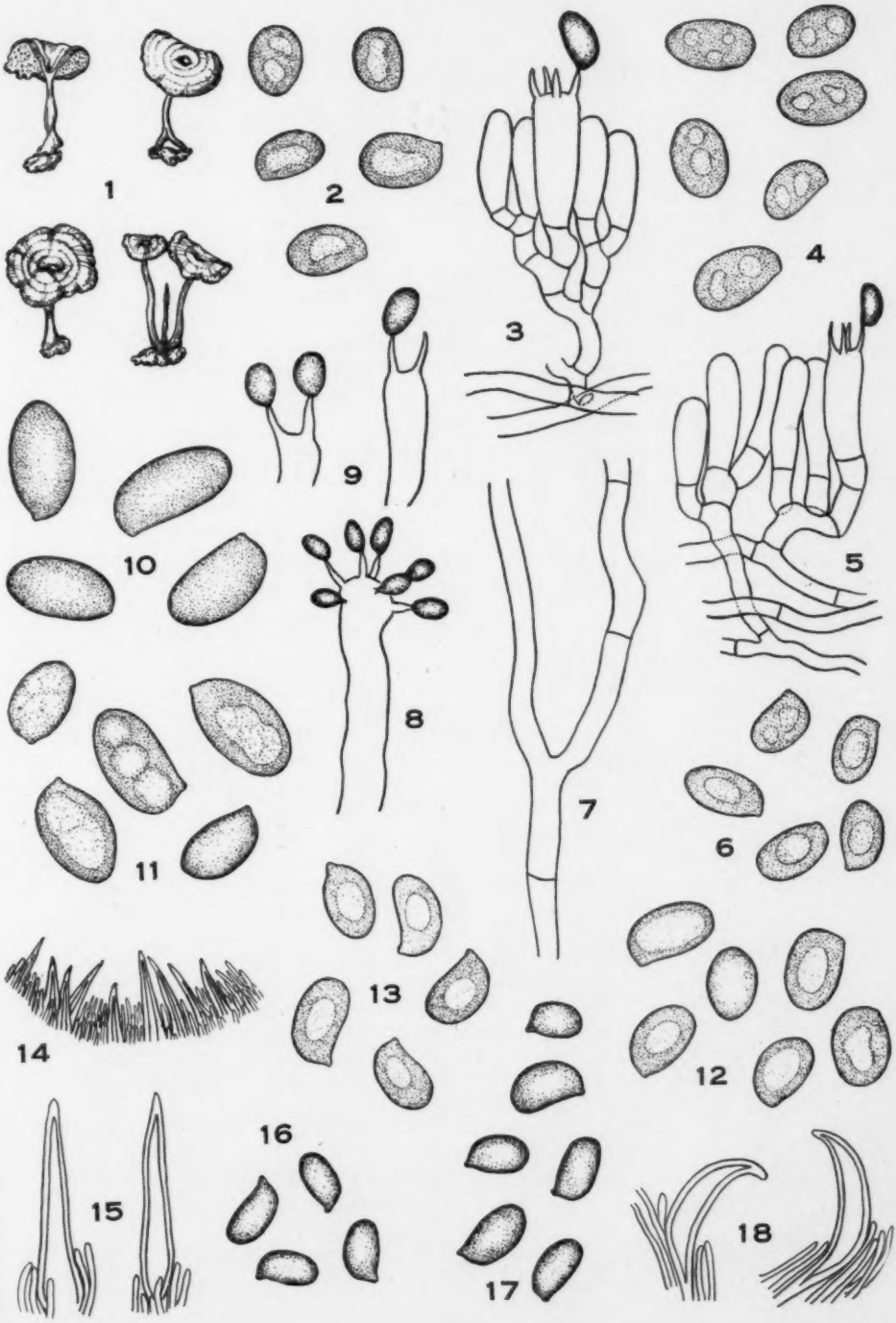


PLATE 22



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